Pc 6118

ISSN 0753-4973

ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

BIBLIOTHÈQUE MUSÉUM PARIS

January-October 1990 Volume 8, N° 3-4

Source : MNHN, Paris

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ALYTES

INTERNATIONAL JOURNAL OF BATRACHOLOGY

January-October 1990 Volume 8, N° 3-4

Alytes, 1989-1990, **8** (3-4): 61-74.

Nomenclature of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons: new proposals*

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In order to homogenize, standardize and simplify the nomenclature of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons, new proposals are made, which rely on a clear separation between the need of a single nomenclatural system at the species level for all living animals, and that of a distinction between different kinds of evolutionary units in nature.

Three major kinds of species-rank taxons can be distinguished in animals: (1) species (s. str.), or bisexual species, with sexual reproduction (including normal meiosis, usually with recombination, fertilization of egg by sperm, and non-clonal inheritance); (2) kleptons, which depend on sexual parasitism for their reproduction, and which include zygokleptons (with sexual reproduction, "hybridogenetic" meiosis, fertilization of egg by sperm, and hemiclonal inheritance) and gynokleptons (with parasexual reproduction, modified meiosis or ameiosis, gynogenesis, and clonal inheritance); (3) klonons, with parasexual or asexual reproduction, modified meiosis or ameiosis or absence of gametes, parthenogenesis or absence of germ, and clonal inheritance. All these evolutionary systematics categories are considered here to be of the same nomenclatural rank within the Linnaean system, that of species, and names of the corresponding taxons should be submitted to the same rules, those of the *International Code for Zoological Nomenclature* for species names. To distinguish kleptons and klonons from species (s. str.), it is suggested to add the abbreviations "kl." and "kn.", respectively, between the generic and the specific names.

* This paper was presented during the symposium on "Nomenclatural treatment of hybrid-derived vertebrate taxa" organised by Andrew H. PRICE as part of the Combined Meeting of the Society for the Study of Amphibians and Reptiles, the Herpetologists' League, Early Life History Section, AFS, the American Elasmobranch Society, with the American Society of Ichthyologists and Herpetologists (Ann Arbor, Michigan, U.S.A., 23-29 June 1988).

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Introduction

Many papers have recently been devoted to the study of several vertebrate "forms" of hybrid origin and that display particular modes of reproduction and of inheritance, such as parthenogenesis, gynogenesis, and "hybridogenesis". The "forms" studied belong to the bony fishes (*Poecilia* and *Poeciliopsis*: see e.g. Schultz, 1977, Monaco, Rasch & Balsano, 1984, Moore, 1984 and Vrijenhoek, 1984; *Phoxinus*: see Dawley, Schultz & Goddard, 1987), the urodeles (*Ambystoma*: see e.g. Bogart, 1982, Bogart & Licht, 1986 and Bogart et al., 1985, 1987), the anurans (*Rana*: see e.g. Dubois, 1977 and Graf & Polls Pelaz, 1989) and the saurians (*Lacerta* and *Cnemidophorus*: see e.g. Cole, 1975, Uzzell & Darevsky, 1975 and Dessauer & Cole, 1986; *Lepidodactylus*: see e.g. Ineich, 1988).

Some, at least, of these "forms" have genetic and evolutionary particularities which distinguish them from "normal species", and several authors have found it necessary to formally recognize these particularities by giving them special "names" or even by ascribing them to new taxinomic[1] categories. The proposals in this respect are diverse, including refusal of any particular nomenclature (Maslin, 1968; Uzzell, 1982; Frost & Wright, 1988), the use of letters or numbers (Schultz, 1961, 1966, 1967; Zweifel, 1965; Cole, 1985; Walker, 1986; Ineich, 1988), the use of compound Latin names (Schultz, 1969, 1977; Cook & Gorham, 1979; Génermont, 1980; Lowcock, Licht & Bogart, 1987), the use of normal simple Latin names between quotation marks (Hubbs & Hubbs, 1932; Günther, 1973; Günther & Hähnel, 1976; Dubois, 1977, 1979; Koref-Santibañez, 1979; Bogart, 1980) and the use of normal simple Latin names preceded by a special mark or sign (Dubois & Günther, 1982).

This diversity of approaches is understandable in the first period of a research, but I feel that we have now reached the time where some standardization is necessary. The proposals made in the present paper are a new contribution towards this aim, which comes after a few other ones and benefits from the comments of various authors (Maslin, 1968; Lazell, 1971; Cook & Gorham, 1979; Mishler & Donoghue, 1982; Cole, 1985; Walker, 1986; Lowcock, Licht & Bogart, 1987; Frost & Wright, 1988; Echelle, 1990 a-b; Frost & Hillis, 1990) on this controversial question.

Some desirable properties of taxinomic systems

Why should we *name* things? I do not think that it is in order to express their "essence", but rather in order to be able to *communicate* about them, to carry some *information* about these things, and in this respect the best nomenclatural system will be the one having the highest generality and universality.

1. I use the correct spellings "taxinomy" and "taxinomic" instead of "taxonomy" and "taxonomic", following Pasteur (1976) and Fischer & Rey (1983).

Source : MNHN, Paris

Systematics is the discipline of biology which has the purpose of *classifying* living beings, that is of ascribing them to *taxons*[2], and of *naming* them.

Systematics is not, or should not be, an intellectual game, or a simple search for intellectual elegance. All biologists need a *taxinomic system* (that is, a classificatory and nomenclatural system) to be able to *communicate* about the living beings they study, and to carry some *information* about these things.

To be theoretically satisfactory and acceptable by all biologists, any taxinomic system should have some properties, among which the following ones can be stressed: unicity, universality, univocality, homogeneity and stability.

(1) *Unicity*: there should be a single taxinomic hierarchy for all living beings, not several.

(2) *Universality*: the taxinomic system should be devised in such a way as to be able to accomodate *all* living beings ever to be found in the real world, not only some of them. This means that taxinomic concepts must bear some determined relationship to *universally observable patterns and particularities* of the organisms of the real world (or of the natural processes involved in the evolution of these organisms), rather than being derived solely from some general *theory*, such as a theory of evolutionary process, or a theory of biological classification.

(3) *Univocality*: the classificatory and nomenclatural system should be univocal, that is, any given living being should unambiguously be ascribed to a given and single place in the system.

(4) *Homogeneity*: there should be some equivalence, by some criteria, between various taxons ascribed to the same category within the taxinomic hierarchy.

(5) *Stability*: the taxinomic system should display at least rather important stability, so that every new discovery should not be liable to modify it partly or totally. This stability should concern both the classificatory pattern and the nomenclature.

THE LINNAEAN SYSTEM

Many different classificatory and nomenclatural systems have been proposed since the beginnings of biology. The only one to have survived for more than two centuries and which, despite various criticisms, is still very healthy, is the Linnaean system of taxinomic hierarchy (a hierarchy of categories) and of Latin binominal nomenclature. Despite its unavoidable limitations, this system has shown until now a great flexibility and has been used with success by biologists having widely divergent ideas of what biological classification should be. Until a better system is ever proposed and shown to be better, any

2. Terms such as "taxon", "phenon", "klepton" or "phylum" are not true ancient Greek or Latin names but modern terms which only bear a formal resemblance to old Greek or Latin names. They should therefore be given normal plurals like "taxons" or "phylums", not artificial ancient Greek or Latin plurals like "taxa" or "phyla". This suggestion follows the advice given in this respect by *The Oxford Guide to the English Language* (ANONYMOUS, 1984: 27): "It is recommended that the regular plural (in *-s*) should be used" [for such words], "even though some are found with either type of plural". Furthermore, for a sake of homogeneity, the term *phylon* should be preferred to "phylum".

Source : MNHN, Paris

taxinomic discussion and proposal should clearly place itself within the frame of the Linnaean system of taxinomic hierarchy and of Latin binominal nomenclature, such as it is recognized and formalized by the International Codes of Nomenclature. This implies in particular that *taxons should have names*, Latin names following the International Rules, and on the reverse that such names should *not* be given to entities which do not qualify as taxons.

On the other hand, acceptance of the Linnaean system does not imply any particular choice as to the philosophy of classification to be used, be it the empiricist, the pheneticist, the cladistic or the evolutionary one. These philosophical choices only have consequences in what concerns classification, but not, at least not directly, nomenclature.

TAXON, PHENON, GENON, PHYLON

When we deal with taxinomy, we deal with the recognition, delimitation, ordering and naming of *taxons*, or taxinomic units. The question must therefore be asked: what is a taxon? According to MAYR (1969: 4), a taxon is a group of organisms which is considered by taxinomists as "sufficiently distinct to be worthy of being assigned to a definite [taxinomic] category". This definition is rather vague and does not help us very much to distinguish taxons from other types of "groups of organisms". But, as a matter of fact, if we ask for more precise definitions, systematists will give us different ones according to the "school" of taxinomy in which they belong. In this respect, it will be useful to examine briefly a few different kinds of "groups of organisms" which may be recognized by systematists.

One such kind is the *phenon*. MAYR (1969) has used this term for a phenotypically reasonably homogeneous sample at the species level. The term *morphospecies* has also been used by some authors for the same category. In a strictly phenetic approach to systematics, the terms taxon and phenon would be equivalent. On the other hand, systematists who take it for granted that a meaningful and "natural" classification of living beings is possible only if based on the study of the phylogenetic and evolutionary relationships between them, that is, cladists and evolutionary systematists, reject the strict correspondence between taxon and phenon, and point to many cases where this correspondence does not hold at all. Several different phenons may be part of a single taxon (the simplest example being that of the males and females of the same species), while on the reverse several different taxons may belong to the same phenon (for example, different dualspecies or sibling species; see BERNARDI, 1980).

Another kind of units which is not often recognized by systematists, but which is of particular relevance to the problems being discussed here, consists of those units which can be recognized on the sole basis of structural genetic similarity. For such genetic units, the new term *genon* would appear convenient. Similarity of genotypes is most unlikely to be a result of convergence between different lineages, and therefore usually a genon is also a taxon. However, in all cases where hybridization is involved, similar genotypes can occur repeatedly through independent hybridization events, and in such cases a genon may not correspond to a single taxon – at least for cladists and evolutionary taxinomists, who

Source : MNHN, Paris

consider that different lineages should be referred to different taxons. Examples of genons which would not, for them, correspond to taxons, would be interspecific hybrids between two species obtained independently by several hybridization events, or, more narrowly, groups of parasexual or asexual individuals shown to have identical electrophoretic markers at some loci, but without evidence (for example from skin grafting experiments) that they originated from the same founder event.

Other kinds of units may be recognized by biologists. I will mention only two examples: (1) "ecotypes" or "ecospecies", characterized by their ecological niches or adaptive zones; and (2) *phylons*, that is, complete lineages or historical entities. The latter are considered by cladists as strictly equivalent to taxons, while for evolutionary systematists taxons are also based on lineages but do not automatically correspond to complete phylons or lineages (whenever genetic, phenetic and ecological divergence has occurred during the history of a phylon, the latter may correspond to several taxons).

NOMENCLATURE OF PARTHENOGENETIC, GYNOGENETIC AND "HYBRIDOGENETIC" TAXONS

Let me now approach the specific problem of the nomenclatural treatment of parthenogenetic, gynogenetic and "hybridogenetic" vertebrate taxons on the basis of these general statements.

First of all, it must be stressed that the problem is: how should we name some particular *taxons*? This excludes from this discussion particular *organisms* which do not qualify as *taxons*. Thus, "hybrids as such", that is, organisms which arose as the individual results of phenomena of hybridization between species or between hybrids, but which do not give rise to particular lineages separated from those of their parental species, do not qualify as parts of independent entities or taxons. They should therefore not be given taxons names, that is Latin binominals written in italics and composed of a generic name and of a specific name, even if these are presented as "informal names". Therefore, for example, instead of *Ambystoma laterale-jeffersonianum*, the corresponding animals should be designated as simple hybrids, as follows: *Ambystoma laterale* × *jeffersonianum*. If "informal systems" are proposed for the designation of individual organisms, these systems should be devised in order to avoid any possible confusion between taxons and non-taxons: therefore they should be based for example on letters or numbers rather than on Latin binominals.

Secondly, for those entities which qualify as taxons, general rules of nomenclature must be devised. These rules must be compatible with the Linnaean system of taxinomic hierarchy and Latin binominal nomenclature, in order to maintain the unicity, universality and homogeneity of this system. They must make sure that *all* the peculiar taxons in question be included in the system, even those which appear rather "atypical" as compared with the "traditional" species concept.

One must avoid confusing two different problems. On one hand, for philosophical reasons of unicity, universality and homogeneity, the nomenclatural system cannot consist of several different, independent and parallel, hierarchies: that is, a simple hierarchy is

Source : MNHN, Paris

required, and, in the Linnaean binominal system, any organism should at least be referable to one taxon of rank genus and to one taxon of rank species. This means that any living organism should be liable to be given a specific name (or two or several, linked by crosses, in the exceptional cases of "hybrids as such"). On the other hand, these philosophical constraints on nomenclature do not bear at all on our understanding of biological phenomena as they occur in nature. There is no philosophical or biological reason why all organisms in nature should belong in similar biological historical entities governed by similar laws: it is perfectly understandable and acceptable that some organisms belong to bisexual species, while others belong to asexual or parasexual taxons. The only constraint which our adherence to the Linnaean system implies is that these asexual or parasexual taxons should in nomenclature be given the rank of species. Homogeneity in the nomenclatural treatment of taxons of the same rank does not imply that these taxons are biologically identical or homogeneous.

Bisexual species and asexual or parasexual "pseudospecies" (as DOBZHANSKY, 1970, called them) all usually belong to well-defined genera. The nomenclature of any of these species-rank taxons consists therefore of a generic name followed by a specific name. The latter should in all cases conform with the rules of the *International Code of Zoological Nomenclature* (ANONYMOUS, 1985), including all the rules about conditions of availability of names, use of type-specimens, priority and homonymy, etc. In many cases, asexual or parasexual taxons of the species rank have been recognized, described and named long before their biological particularities were discovered, and in all these cases, they should retain the names first given to them. In other cases, these taxons should be named by the same procedures as "normal" species.

However, since different types of species-group taxons of the species rank may be recognized in the living world, differing in particular in their modes of reproduction and of inheritance, it appears useful and justified to indicate some of these differences by writing the names of these taxons in a special way. In this respect, several suggestions have been made for the nomenclature of asexually or parasexually reproducing forms, especially among vertebrates of hybrid origins. Some of these suggestions, for example the use of letters such as A, B or C, or of symbols such as Cx, Cy or Cz, may be rejected immediately, as non-Linnaean. Other ones include the placement of the species-group name of these taxons between quotation marks, and the use of compound names indicating the basic genotype of these forms. I discussed elsewhere with Rainer GÜNTHER the reasons for rejecting these proposals, and we proposed another system (DUBOIS & GÜNTHER, 1982). We suggested that names of "atypical" species-rank taxons such as kleptons should be simple, not compound, Latin names, but that attention should be drawn to the particularities of these taxons by placing a special symbol between the generic name and the specific name of such taxons. Thus for example, in the case of kleptons, the abbreviation "kl.": *Rana* kl. *esculenta*.

THREE DIFFERENT KINDS OF SPECIES-RANK TAXONS

How many different types of species-rank taxons can we recognize in animals? I suggest that, despite the vast diversity of local and particular situations, all cases can be

Source : MNHN, Paris

referred to three major categories, one of which itself includes two rather distinct subcategories. However, before presenting these categories in more detail, I wish to make two preliminary comments.

The first comment concerns the use of the term *hybridogenesis*. This use is extremely confusing for several reasons. First of all, this term has been used for a very long time in the biological literature to designate the simple phenomenon of appearance of a hybrid through hybridization of two organisms belonging to two different taxons. On the other hand, SCHULTZ (1969) proposed to use the same term to designate a particular type of reproduction, which occurs in some *Poeciliopsis* of hybrid origin. This second meaning is completely different from the original one. For this reason, BORKIN & DAREVSKY (1980) proposed the replacement name *creditogenesis* for the concept called hybridogenesis by SCHULTZ (1969).

But, besides this homonymy problem, both SCHULTZ's hybridogenesis and BORKIN & DAREVSKY's creditogenesis are confusing for a second reason: they are defined as "a reproductive mechanism", and most authors tend to view them as concepts similar to those of gynogenesis or parthenogenesis, which bear similar names. But the latter concepts designate particular modes of *starting the development of an egg*, and they do not imply by themselves any particular kind of meiosis: while gynogenetic or parthenogenetic taxons do indeed have particular kinds of meioses, which give rise to particular types of eggs, parthenogenesis or gynogenesis can also occur sometimes spontaneously, or can be artificially induced, in normal bisexual species and in normal eggs. On the other hand, hybridogenetic reproduction involves only a particular kind of gametogenesis, while the starting of egg's development follows a normal pattern (with fertilization). For this reason, I think it useful to dissociate the concept of "reproductive mechanism" into two distinct concepts: (1) mode of formation of gametes, or *gametogenesis*; and (2) mode of starting of egg's development, for which I propose the general term of *germinogenesis* (from the Latin *germen*, which gave "germ", the term by which embryologists call the active egg starting its development, divisions, etc.). Usually germinogenesis occurs by fertilization, which gives rise to a zygote, and can also be called *zygogenesis*. Other kinds of germinogenesis are *gynogenesis* (the sperm stimulating the egg to develop without true fertilization) and *parthenogenesis* (development of a virgin egg, which can be started by various factors).

In what follows, I am provisionally retaining the term hybridogenesis, since it is now well established, but in a restricted sense: rather than a "mode of reproduction", it means here a particular type of gametogenesis which, whatever its cytological mechanisms may be (actually there apparently exist several of them, and even rather distinct ones), results in the exclusion of one complete (or almost complete) parental chromosome set and in the formation of a gamete having a pure (or almost pure) chromosomal complement from the other parental species.

Now to the second comment. What should be the criterions for deciding that a particular asexual or parasexual form, with clonal or hemiclonal inheritance, is a taxon of species rank? These criterions will depend on the philosophical school of biological classification chosen. For systematists of the phenetic school, overall phenetic and genetic similarity will be the major criteria. For systematists of the cladist school, any lineage resulting from a given founder event will be afforded taxinomic recognition, and lineages

Source : MNHN, Paris

resulting from distinct founder events will be considered distinct taxons. Finally, for evolutionary systematists, the latter condition also applies, but on the other hand when a major phenetic, genetic and/or ecological shift has occurred within a single lineage as a result of mutation, it may be warranted to recognize distinct taxons within this lineage.

Now I shall present briefly the three major types of species-rank taxons which I suggest to distinguish in animals, and which I had already pointed out briefly in a previous paper (DUBOIS & GÜNTHER, 1982: 294-295). Despite the vast array of particular cases observed in nature, it seems that the three categories here defined (including one with two rather distinct subcategories) cover all possible cases in existence in the real world.

(1) *Species* (s. str.), or bisexual species.

(2) *Kleptons*, with two subcategories:

(a) "Hybridogenetic" and zygogenetic kleptons, or *zygokleptons*, with zygogenesis and hemiclonal mode of inheritance.

(b) Gynogenetic kleptons, or *gynokleptons* (or *klonokleptons*), with gynogenesis and clonal mode of inheritance.

(3) *Klonons*, that is, all kinds of uniparental "species" with clonal heredity *not* depending on sperm for their reproduction, including, both, species with truly asexual reproduction (for example vegetative reproduction), and species with parasexual or asexual clonal reproduction (for example, autofertilization, thelytoky).

DUBOIS & GÜNTHER (1982) also proposed to recognize as a *synklepton* a group of forms including both one (or several) klepton(s) and the "good species" from which it (they) originated. Similarly, I propose here to call *synklonon* any group of forms including both one (or several) klonon(s) and the "good species" which gave birth to it (them).

If one accepts DUBOIS & GÜNTHER's (1982) proposal to use a sign, intercalated between the names of generic and specific rank, to recognize these special species-rank taxons, different signs should be used for the different types of taxons, in order to avoid any possible confusion. DUBOIS & GÜNTHER (1982) proposed the abbreviations "kl." and "synkl." respectively for klepton and synklepton; these signs, or one of them, were used by a few authors since then (DUBOIS, 1982, 1983, 1984; GÜNTHER, 1983, 1987; GÜNTHER & KOREF-SANTIBAÑEZ, 1983; BURNY & PARENT, 1985; MONNEROT, DUBOIS & TUNNER, 1986; OHLER, 1987, 1989; POLLS PELAZ, 1987, 1988; BERGER & GÜNTHER, 1988; GÜNTHER & PLÖTNER, 1988; PLÖTNER, GÜNTHER & SCHADE, 1988; CRESPO, OLIVEIRA & PAILLETTE, 1989; GRAF & POLLS PELAZ, 1989; POLLS PELAZ & GRAF, 1989). I here propose the abbreviations "kn." and "synkn." respectively for klonon and synklonon.

The principal characteristics of interest to systematists of the types of taxons defined above are shown in Table I. Both species (s. str.) and klonons are reproductively independent, while both zygokleptons and gynokleptons depend on sexual parasitism for their reproduction (and for their survival) and are therefore not reproductively independent. Both gynokleptons and klonons display a clonal mode of inheritance, while zygokleptons have a hemiclonal one.

Source : MNHN, Paris

Table I. – The principal genetic and reproductive characteristics of the different evolutionary taxinomic categories of species rank: species (s. str.), klepton (zygoklepton and gynoklepton) and klonon.

Name and symbol	Species (s. str.)	Klepton (kl.) Zygoklepton (zykl.)	Gynoklepton (gykl.)	Klonon (kn.)
Examples		*Poeciliopsis, Rana*	*Poeciliopsis*	*Cnemidophorus, Lacerta*
Sexes	Both	♀ or both	♀	♀
Free intrabreeding	Yes	No	No	No
Reproduction	Sexual	Sexual	Parasexual	Parasexual or asexual
Gametogenesis	Normal meiosis (usually with recombination)	"Hybridogenesis": modified meiosis or ameiosis	Modified meiosis or ameiosis	Modified meiosis or ameiosis or absence of gametes
Germinogenesis	Zygogenesis (fertilization)	Zygogenesis (fertilization)	Gynogenesis (pseudo-fertilization)	Parthenogenesis or absence of germ
Sperm necessary	Yes	Yes	Yes	No
Sexual parasitism	No	Yes	Yes	No
Reproductive independence	Yes	No	No	Yes
Mode of inheritance	Not clonal (recombination between parental genomes)	Hemiclonal (clonal inheritance of one parental genome)	Clonal	Clonal

FINAL QUESTIONS

Two remaining problems are worth discussing before concluding

(1) Should gynogenetic forms be included in the category klepton or in the category klonon? A purely formal genealogical approach to taxinomy would lead to include them in the category klonon, since they have the same clonal mode of inheritance as parthenogenetic forms For those who would favor such an approach, the categories and subcategories listed above and shown in Table I could be arranged differently, as follows: (1) *species*; (2) *zygokleptons* (or *kleptons* s. str.); (3) *klonons*, with two subcategories, (a) *gynoklonons* (or *kleptoklonons*), equivalent to *gynokleptons* in Table I, and (b) *parthenoklonons*, equivalent to *klonons* in Table I.

But, as an evolutionary systematist, I think that the fact that gynogenetic forms depend on the sperm of another species and are therefore not reproductively independent is very important and should be stressed by placing them in the category klepton: their

Source MNHN, Paris

dependence on the sperm of another species implies for these forms the inability to escape from the geographical range of that species, and the extinction of the latter also results in their own extinction True parthenogenetic forms are very different from them in not having these limitations

Furthermore, gynogenetic forms use sperm for their reproduction, and there is always some danger in using sperm. even if you don't want to, you run the risk of being fertilized, and this is indeed what occurs for example in some *Phoxinus* gynokleptons or in some *Ambystoma*

Finally, it should be stressed that the same synklepton can include both zygokleptons and gynokleptons (see for example the *Poeciliopsis occidentalis* synklepton), which stresses the fact these two kinds of taxons are closely related and that the passage from one to the other one is easy.

(2) Should zygokleptons be considered taxons of the species-rank or of a lower rank? This question may be asked if we consider for example WILEY's (1978) definition of the evolutionary species as "a lineage of ancestral descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendancies and historical fate". Strictly speaking, zygokleptons are not true lineages but half-lineages[3], and for their "second half" they do not maintain identity from the lineage which provides the genetic material, nor do they have their fully independent evolutionary tendancies and historical fate, since their history is directly related to the history of the species on which they depend for their perpetuation. I can see three possible solutions to this problem.

One would consist in considering a klepton as formally being part of the ancestral bisexual species which provided the part of its genome which is clonally transmitted in the klepton. Another one would consist in considering it as formally being part of the bisexual species which allows its perpetuation (and which is also usually, but not always, one of the ancestral species from which it arose by hybridization). In both these symmetrical cases, the klepton category would be a category of subspecific, and not specific, rank, and names of kleptons would be written in the following way: *Rana lessonae* kl. *esculenta*.

The third solution, which I already advocated (DUBOIS & GÜNTHER, 1982), is to consider kleptons as taxons of specific rank, but to indicate the fact that they belong in a wider genetic system by referring them, as well as the bisexual species with which they interact genetically, to more comprehensive taxons, of a rank intermediate between genus and species, and which we proposed to call synkleptons: *Rana* (synkl. *esculenta*) kl. *esculenta*.

This system has the advantage of allowing for the possibility of still recognizing taxa of subspecific rank within kleptons (see MASLIN, 1968 and DUBOIS & GÜNTHER, 1982), which the first one does not allow Furthermore, it poses no particular problems within the

3. I here disagree with ECHELLE (1990 a b) who recently suggested that "hybridogens" are full lineages, because "a historical group of hybridogens is connected to an ancestral hybrid individual by haploid genealogical lines (= lineages)" (ECHELLE, 1990 a 111) This is true, but the same group is also connected to the species with which it has to backcross at each generation any "hybridogenetic" offspring derives its genome from two parents It is irrelevant in this respect to point that "in hybridogens, the traits expressed by the species providing the 'borrowed' genome are not entrained in the germ line" [of the "hybridogen"] (ECHELLE, 1990 a. 111). These traits are also transmitted by a germ line, that of the "parasitized" species We should not forget that we are classifying living *organisms*, not germ lines, or, put in other words, that the object of taxinomy is the *soma*, not the *germen*

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frame of Linnaean nomenclature, while the first one poses problems when the kleptic name happens to be nomenclaturally older than the specific one (this is the case in the example used above: *lessonae* Camerano, 1882 would have priority over *esculenta* Linné, 1758). For these reasons, I here maintain my support to the nomenclatural system first proposed by DUBOIS & GÜNTHER (1982).

CONCLUSION

The recognition of the three distinct evolutionary taxinomic categories of species (s. str.), klonon and klepton (the latter with the two subcategories of zygoklepton and gynoklepton), three categories considered here to be of the same nomenclatural rank (that of species), should clarify discussions on the problems of nomenclature of taxons belonging to the second and third of these categories. The proposals made here, in particular that of adding a sign (kn or kl.) between the generic and specific name, are currently not acceptable within the rules of the *Code* now in force (ANONYMOUS, 1985). Such rules are however liable to be modified, if zoologists feel that the proposals made above are useful, and apply to the International Commission on Zoological Nomenclature for such a modification. The rules have already been changed many times to incorporate new proposals, for example, recently, concerning the nomenclature of some infrageneric and supraspecific taxons (see e.g. BERNARDI, 1980), and could well be modified as well in this case.

RÉSUMÉ

De manière à homogénéiser, standardiser et simplifier la nomenclature des taxons parthénogénétiques, gynogénétiques et "hybridogénétiques" de Vertébrés, de nouvelles propositions sont faites, qui s'appuient sur une séparation nette entre le besoin d'un système nomenclatural unique pour tous les animaux au niveau spécifique, d'une part, et celui d'une distinction entre différents types d'unités évolutives existant dans la nature, d'autre part.

Trois types principaux de taxons de rang spécifique peuvent être distingués chez les animaux: (1) les espèces (s. str.) ou espèces bisexuées, à reproduction sexuée (comportant une méïose normale, avec habituellement recombinaison génétique, fécondation de l'oeuf par un spermatozoïde et hérédité non-clonale); (2) les kleptons, qui dépendent d'un parasitisme sexuel pour leur reproduction, et qui comportent d'une part les zygokleptons (à reproduction sexuée, avec méïose "hybridogénétique", fécondation de l'oeuf par un spermatozoïde et hérédité hémiclonale) et d'autre part les gynokleptons (à reproduction parasexuée, avec méïose modifiée ou absente, gynogenèse et hérédité clonale), (3) les klonons, à reproduction parasexuée ou asexuée, avec méïose modifiée ou absente ou gamètes absentes, parthénogenèse ou absence de germe, et hérédité clonale. Toutes ces catégories de systématique évolutive sont ici considérées comme étant du même rang nomenclatural au sein du système linnéen, le rang spécifique, et les noms des taxons correspondants devraient être soumis aux mêmes règles, celles du *Code International de Nomenclature Zoologique* pour les noms spécifiques. Pour distinguer les kleptons et les

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klonons des espèces (s. str.), il est suggéré d'ajouter les abréviations "kl." et "kn.", respectivement, entre les noms générique et spécifique.

ACKNOWLEDGEMENTS

For their suggestions and comments on first drafts of this manuscript, I am grateful to Claude DUPUIS, Anthony A ECHELLE, Annemarie OHLER, Manuel POLLS PELAZ and an anonymous reviewer.

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Corresponding editor: Andrew H. PRICE

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Source MNHN, Paris

Alytes, 1989-1990, **8** (3-4): 75-89.

The Biological Klepton Concept (BKC)*

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The proposal of DUBOIS & GÜNTHER (1982) to create a new systematic category (klepton) embracing the hybridogenetic and gynogenetic taxa (sensu lineages, genealogies) is analyzed. Such taxa can be considered neither as simple hybrids nor as good species.

Biological trends for all known kleptons in the *Ambystoma*, *Rana*, *Phoxinus*, *Poecilia* and *Poeciliopsis* complexes are summarized, and their new associated terms discussed.

Kleptons are historical entities, but not of the classical Biological Species Concept (BCS sensu MAYR, 1982), but showing equally ecological, genetical, and evolutionary relevances as their associated " good " species.

From an epistemological point of view, the fact that so-called kleptons are not subject to cladistic laws (because kleptons are polyphyletic), must not be considered as and argument for ignoring the existence of those taxa, either biologically or taxonomically.

Klepton evolutionary rules, as parallel species pathways, are discussed: we conclude that not all evolutionary processes take place in the species context.

The Biological Klepton Concept (BKC) is proposed: a klepton is a community of populations with a hybrid genome derived from the same parental species, reproductively dependent upon sympatric species that play the rôle of sexual host.

" But what about viruses ? Can they be classified in Linnean fashion ? (...) The only attribute of life possessed by viruses is reproduction with genetic continuity and the possibility of mutation. Evolution can therefore occur. " (GOODHEART, 1969, 38).

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* This paper was presented during the symposium on "Nomenclatural treatment of hybrid-derived vertebrate taxa " organised by Andrew H PRICE as part of the Combined Meeting of the Society for the Study of Amphibians and Reptiles, the Herpetologists' League, Early Life History Section, AFS, the American Elasmobranch Society, with the American Society of Ichthyologists and Herpetologists (Ann Arbor, Michigan, U S A , 23-29 June 1988).

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Natural taxa must be named

I suppose all evolutionary biologists agree with this statement, in spite of rare biological characteristics or atypical reproductive modes in taxa of certain lineages The example of viruses is very clear: we don't know if it can be said that viruses are alive (they have no intrinsic metabolism), but viruses do have names becauses they constitute historical entities (acting as genetical cell parasites of animals and plants), and names are needed to facilitate studies on them.

Parthenogenetic, gynogenetic, and hybridogenetic populations constitute special taxa in the Animal Kingdom. Briefly it can be said that parthenogenetic unisexual females reproduce without sperm, whereas gynogenetic unisexual females need sperm of associated species for reproducing, the genome of which is not included into the egg after fertilization; finally, hybridogenetic taxa need either the sperm or the ovocytes of associated species for reproducing, the genome of which is incorporated into the egg. The analogy with respect to viruses is clear: as viruses are genetic parasites of cells (the biological unit, Mayr, 1982), thus gynogens and hybridogens are genetic parasites of " good " species (the unit of evolution, Mayr, 1982).

Nomenclature of parthenogenetic, gynogenetic, and hybridogenetic taxa is a systematic topic currently of major interest, due to biological paradoxes in those populations which put in question the classical concept of species. Discussions at the Ann Arbor meeting made evident that:

(1) Parthenogenetic population must be named and considered separately from gynogenetic and hybridogenetic populations.

(2) Parthenogenetic populations are genetically autonomous, constituting taxa with clonal genetic inheritance, and frequently with hybrid origin as their primary speciation event (see discussions in Cuellar, 1987). Parthenogenetic reproduction is asexual (sensu Maynard Smith, 1986) and automitic (sensu Mogie, 1986).

(3) Gynogenetic and hybridogenetic populations do not constitute genetically autonomous taxa They reproduce sexually, with well-established mechanisms of mating choice (see for instance Blankenhorn, 1977; Keegan-Rogers & Schultz, 1988)

(4) Gynogenetic and hybridogenetic populations cannot be included in the Biological Species Concept (BSC, sensu Mayr, 1942, 1982).

It is my wish to consider in this paper only nomenclatural treatment for gynogenetic and hybridogenetic taxa. Biological characteristics concerning reproductive modes, gametogenetic mechanisms, hybrid genome composition, ploidy, and sexual parasitism, for different gynogenetic and hybridogenetic taxa are reviewed and summarized as they occur in fishes and amphibians.

Major controversies concerning nomenclatural treatment of gynogenetic and hybridogenetic taxa have originated from ambiguous discussions on their conformance (or not) with the unitary concept of species. I here show that the biological characteristics of those taxa are quite unitary, but far different from those of the BSC. Accordingly, I propose

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herein a Biological Klepton Concept (alternative to BSC). Kleptons are regarded as distinct, natural, and real biological entities, extrapolating from the term and systematic category created by DUBOIS & GÜNTHER (1982).

THE DEFINITION OF KLEPTON GIVEN BY DUBOIS & GÜNTHER (1982)

The aim of these two authors was " . .to provide a general name and nomenclatural rules for some particular animal ' forms ' which cannot be properly considered as ' biological ' species, such as gynogenetic and hybridogenetic unisexual fish of the genus *Poeciliopsis*, gynogenetic unisexual fish of the genus *Poecilia*, gynogenetic unisexual salamanders of the genus *Ambystoma*, and hybridogenetic (or leaky hybridogenetic) frogs of the genus *Rana*. All these forms, despite their diversity, have the following features in common: they are of hybrid origin; their heredity is clonal or hemiclonal; for their reproduction such forms depend on the gametes of a distinct ' good ' species. " (DUBOIS & GÜNTHER, 1982: 290).

From a practical point of view, creation of the new term *klepton* provides simplicity, ready dichotomy, university of application and a precedent for naming further, still unknown categories of taxa.

From an evolutionary point of view, the term klepton excludes the Biological Species Concept, and connotes a new one, the Biological Klepton Concept.

From a genetical, ecological, and ethological point of view, the term klepton implies the hybrid genetic character of its taxa, as well as their reproductive modes that involve a genetical parasitism of hybrids on their " good " associated parental species. Special mate choice ethograms and ecological niches are involved in the klepton concept.

All of these biological characteristics are entailed in use of the term klepton, which nomenclaturally can just be introduced as an abbreviation between the binomial terms, i.e.: *Rana* kl. *esculenta, Poecilia* kl. *formosa.*

KLEPTONS ARE NOT SPECIES

" Species are groups of actually or potentially interbreeding natural populations which are reproductively isolated from other groups. " (MAYR, 1942: 120).

" An evolutionary species is a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies. " (SIMPSON, 1961: 153).

" A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature. " (MAYR, 1982: 273).

To my knowledge, Ernst MAYR never considered specifically in his works the cases of hybridogenetic and gynogenetic populations. In fact findings concerning these taxa are very recent and their biological interest remains still ignored in general zoological books.

Source MNHN, Paris

However, the father of the BSC clearly separated parthenogenetic taxa from parameters of the unitary species: " The biological species concept is based on the reproductive isolation of populations. The concept, therefore, cannot be applied in groups of animals and plants that have abandoned bisexual reproduction. " (MAYR, 1982. 283).

In contrast to MAYR, several authors (as FROST & WRIGHT, 1988) have proposed solutions for naming parthenogenetic taxa, considering them as species, from cladistic points of view: " ... a lineage concept, later redefined by WILEY (1978) as the largest monophyletic group whose components are not irretrievably on different phylogenetic trajectories ". Reading WILEY (1978), however, one concludes that FROST & WRIGHT (1988) merely present an interpretation of WILEY's evolutionary concept of species (modified from SIMPSON, 1961), not of anatomically unisexual taxa.

The systematic protocol for hybridogenetic and gynogenetic populations thus remains indeterminate. Those taxa are neither asexual as parthenogens, nor reproductively isolated bisexual populations as species. Nevertheless, it is true that some gynogenetic populations reproduce clonally, in analogy to parthenogens. But gynogenetic populations cannot reproduce alone and reproductive isolation is the major biological requirement of autonomous population taxa The point of major importance in classification is the mode of reproduction (that is, genetic parasitism common to hybridogens and gynogens), not the mode of conservation of the genotypes (clonal as in gynogens and parthenogens, hemiclonal or clonal in hybridogens)

BIOLOGICAL CHARACTERISTICS IN KLEPTONS

Kleptons are real entities.

Biological trends in all known gynogenetic and hybridogenetic vertebrate hybrid taxa are summarized in Table I, showing clear analogies between various fish and amphibian complexes. Some very interesting findings concerning " before meiosis ", " pre-meiotic ", and " ameiotic " cytogenetic events, for different complexes, are of major cytological and evolutionary interest These phenomena could be interpreted as convergent solutions to hybridity (from a darwinistic point of view), or as a result of neutral mutations in ancestors, before hybridization, well utilized after casual hybridization by gynogens and hybridogens for their reproduction (random walk evolution of the parental species genome, sensu KING & JUKES, 1969, followed by natural selection on hybrids, sensu DOBZHANSKY, 1937).

It is worth noticing that constant presence of some parental genomes have been found in all complexes (the genome " laterale " in *Ambystoma* kleptons, as well as the presence of the genome "ridibunda " in all *Rana* kleptons, or the presence of the genome " monacha " in all *Poeciliopsis* kleptons).

In all cases, the presence of a sexual host associated with each klepton is a clear and distinct fact for all these hybrid taxa.

However, no gynogenetic or hybridogenetic taxa have yet been found in reptiles, where are least 30 parthenogenetic lizard taxa exist (CUELLAR 1987).

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Another meaningful reason for considering a common nomenclatural treatment for gynogens and hybridogens is that the *Poeciliopsis* complex includes both hybridogenetic and gynogenetic taxa (see Table I). Likewise it appears (as inferred from the results of BOGART et al., 1987) that gynogenetic and hybridogenetic reproductive modes occur in the very same hybrid individuals, in some populations of *Ambystoma*.

A NEW, MORE GENERALIZED DEFINITION OF KLEPTON : THE BIOLOGICAL KLEPTON CONCEPT (BKC)

The definition of klepton given by DUBOIS & GÜNTHER (1982) was based on three conditions that do not always take place in all hybridogenetic and gynogenetic hybrid taxa. For instance recombinant gametes occur in low frequencies in some rare *Rana* kl. *esculenta* hybridogenetic populations, as well as diploid gametes containing both parental genomes (GRAF & POLLS PELAZ, 1989). In these cases the original definition of klepton would not apply.

Thus I propose a more extensive Biological Klepton Concept: " A klepton is a community of populations with a hybrid genome derived from the same parental species, reproductively dependent upon sympatric species that play the role of sexual host ". An equivalent definition would be: " A klepton is an evolutionary systematic category (parallel to the species pathway) including hybrid populations reproducing by hybridogenesis and gynogenesis ".

I nevertheless agree completely with MAYR (1982) in considering the species as the unit of evolution, as well as the cell is the functional biological unit of life. The analogy of viruses and kleptons, stated previously, reminds how carefully the evolutionary relevance of both groups must be considered, especially of retroviruses and allopolyploid kleptons.

NAMED, AND STILL UNNAMED KLEPTONS

" I don't like to see descriptions of the Evolution as the mean of survival and multiplication of DNA. (...) It would be as absurd as to propose explanations of Eastern literature as the means of survival of the points on the letter i. " (translated from MARGALEF, 1980. 93).

Kleptons could be named in the same way as viruses, using combined numbers or letters referring to their prevailing genomes (transmitted clonally, hemiclonally, or recombined). But kleptons are animals, they are clearly alive, and they have phenotypes analogous to those of the " good " species described by LINNAEUS

In fact one of the reasons prompting DUBOIS & GÜNTHER (1982) to propose the new term klepton was the fact that binomials at the Linnaean fashion already exist for many of those taxa. That is, some kleptons were named as species, and their morphological description and names were available before the discovery of their hybrid character and

Source MNHN, Paris

Table I. Biological trends for some gynogenetic and hybrid genetic taxa. Major papers and reviews concerning each topic are referred to by numbers:

(1) SCHULTZ (1969) ; (2) FERRIS (1984) , (3) VRIJENHOEK (1984) ; (4) CIMINO (1972a) , (5) CIMINO (1972b) ; (6) SCHULTZ (1977) ; (7) MOORE (1984) , (8) HUBBS & HUBBS (1932) , (9) RASCH et al. (1982) , (10) MONACO et al (1984) , (11) DAWLEY et al. (1987) , (12) DAWLEY & GODDARD (1988) ; (13) GODDARD et al (1989) , (14) BERGER (1977) , (15) GRAF & MÜLLER (1979) , (16) HEPPICH et al (1982) , (17) POLLS PELAZ (1991) , (18) TUNNER (1974) , (19) GRAF & POLLS PELAZ (1989) , (20) GRAF et al. (1977) , (21) UZZELL & HOTZ (1979) ; (22) UZZELL (1964) , (23) MASLIN (1968) , (24) LOWCOCK et al (1987) , (25) KRAUS (1985) , (26) BOGART et al (1989) , (27) UZZELL & GOLDBLATT (1967) , (28) SERVAGE (1979) , (29) UZZELL (1970) , (30) MACGREGOR & UZZELL (1964) , (31) CUELLAR (1976) , (32) DOWNS (1978) , (33) UZZELL & GOLDBLATT (1967) , (34) LYNCH (1984) , (35) UZZELL (1969) , (36) MORRIS & BRANDON (1984) , (37) BOGART et al (1985) , (38) BOGART & LICHT (1986) ; (39) MORRIS (1985)

Kleptic nomenclature		Parental genome	Gametogenesis	Reproduction mode	Sexual host
Fishes: *Poeciliopsis* complexes					
Precedent nomenclature: hyphenated names,					
Poeciliopsis kl *monachalucida* Schultz, 1969$_2$	2n	mon , luc$_3$	Premeotic exclusion$_{4,1,5}$	Hybridogenesis$_{3,1,6}$	*P lucida*$_{3,6}$
	3n		Endomitosis$_{4,5}$	Gynogenesis$_{3,1,6}$	*P lucida, P. monacha*$_{3,6}$
Poeciliopsis kl. *monachaoccidentalis* Schultz,1971$_2$	2n	mon , occid $_3$	Prem exclusion$_{4,5}$	Hybridogenesis$_{3,6}$	*P occidentalis*$_{3,6}$
Poeciliopsis kl *monachalatidens* Schultz,1971,	2n	mon , latid $_3$	Prem. exclusion$_4$	Hybridogenesis$_{3,6}$	*P latidens*$_{3,6}$
Unnamed *Poeciliopsis* klepton	2n	(mon.-vir), luc $_3$	Prem. exclusion ?	Hybridogenesis$_{3,7,6}$	*P lucida* ?$_{3,6,7}$
Unnamed *Poeciliopsis* klepton	3n	mon., vir., luc.$_3$	Endomitosis ?	Gynogenesis$_{3,6}$	*P virtosa*$_{3,6}$
Fishes: *Poecilia* complex					
Poecilia kl. *formosa* (Girard, 1859)$_2$	2n	mex., latip.$_8$	Apomixis$_{9,10}$	Gynogenesis$_{10}$	*P. mexicana*$_{10}$
	3n				*P latidens*$_{10}$
Fishes: *Phoxinus* complexes					
Unnamed *Phoxinus* klepton	2n	eos, neogaeus$_{11,12,23}$	(?)	Gynogenesis$_{1,12}$	*P. eos*
	3n			Hybridogenesis ?$_{12,13}$	*P. eos, P. neogaeus*

Source : MNHN, Paris

Amphibians: *Rana* complexes Precedent nomenclature: formal names[2]					
Rana kl. *esculenta* Linnaeus, 1758[2]	2n		Before-meiosis exclusion[15]		*R. ridibunda* *R. lessonae* [9]
		rid., less.[14]	+ endomitosis[16]	Hybridogenesis[18]	
	3n		Idem, and amiosis[17]		*R.* kl. *esculenta*
Unnamed *Rana* klepton	2n	rid., perezi[20]	B-meiosis excl.?	Hybridogenesis[20]	*R. perezi*
Unnamed *Rana* klepton	2n	rid., bergeri[21]	B-meiosis excl.?	Hybridogenesis[21]	*R. bergeri*
Amphibians: *Ambystoma* complexes Precedent nomenclature: formal names[22,23] and hyphenated names[24]					
Ambystoma kl. *nothagenes* Kraus, 1985	3n[24],4n[26]	lat., tex., tigr.[26]	(?)	(?)	*A. tigrinum*? *A. laterale*?[25]
Ambystoma kl. *platineum* (Cope, 1867)[2]	2n[24],3n[22,27],4n[24]	lat., jeff.[27,28]	Endomitosis[22,29,30,31]	Hybridogenesis[32] Gynogenesis?[22,27,34,30] Parthenogenesis?[35,32,25]	*A. tigrinum*? *A. texanum*?[22,36,32] *A. jeffersonianum*?[22] *A. maculatum*?[36]
Unnamed *Ambystoma* klepton	2n,3n[37,38,32],4n[26,32]	lat., tex.[37,38]	(?)	(?)	*A. laterale*? *texanum*?[37]
Unnamed *Ambystoma* klepton	3n[39]	lat., jeff., tigr.[39]	(?)	(?)	
Unnamed *Ambystoma* klepton	3n,4n[36,24]	lat., jeff., tex.[36,24]	(?)	(?)	

Source : MNHN, Paris

reproductive mechanism (hybridogenesis or gynogenesis). It was the case of *Rana* kl. *esculenta* Linnaeus, 1758, *Ambystoma* (Cope, 1867), and *Poecilia* kl. *formosa* (Girard, 1859). Current authors continue to use those ancient names, and DUBOIS & GÜNTHER (1982) proposed simply to introduce the abbreviation " kl. " in the binomial to distinguish them from species.

Thus the major nomenclatural controversies that now occur concern kleptons that still are unnamed.

Several papers have been published concerning these topics, and the dilemma involves two major alternatives: the use of hyphenated names as proposed by SCHULTZ (1969), and the use of DUBOIS & GÜNTHER's (1982) klepton nomenclature.

Hyphenated nomenclature consists in giving all parental names of genomes composing the hybrid, each one being preceded by a number indicating the ploidy level of each genome (for instance *Ambystoma laterale-(2)jeffersonianum-tigrinum*). This is a genetic systematic point of view.

I choose the klepton nomenclature because I consider that system as most practical from an evolutionary, general biological and phenotypical points of view. The klepton nomenclature lets us treat separately each case with different binomial, just introducing the particle " kl. " between. But it also implies that authors studying different hybridogenetic and gynogenetic hybrid taxa must undertake careful description of all known kleptons. Fully complete description is needed, including morphology. For instance in European complexes of *Rana* there are two quite well genetically known kleptons yet unnamed. That constitutes an additional difficulty for people concerned for their conservation, ecological study and zoogeographical considerations.

In the absence of complete descriptions of kleptic taxa, provisional names could be employed. For instance GRAF & POLLS PELAZ (1989) utilize *Rana* kl. RP (*Rana ridibunda-perezi* sensu SCHULTZ 1969) for referring to one still unnamed Southern Europe hybrid. Either SCHULTZ's hyphenated names or other lettered or numbered nomenclatures could be provisionally accepted until formal kleptic names are substituted, once complete descriptions of those taxa are provided.

WHEN IS A NEW KLEPTON JUSTIFIED ? THE PROBLEM OF POLYPLOIDS

Biological characteristics of *Ambystoma* kl. *nothagenes* Kraus, 1985, are noted in Table I. I know that Canadian workers on the *Ambystoma* complex disagree with consideration of this taxon as a separate species (BOGART & LICHT, 1986; LOWCOCK et al., 1987). They are correct. It is not a species but a klepton. Kleptic nomenclature and the BKC concept should substitute for the BSC The case is a classic illustration of conditions justifying the erection of a new klepton.

As a klepton is the result of hybridization between two or more species, all new discoveries of hybrids should be nomenclaturally recognized. Thus the discovery by KRAUS (1985) of triploid hybrids with parental genomes of *Ambystoma laterale*, *A.*

Source MNHN, Paris

texanum, and *A. tigrinum* was a biological novelty (no other combination of those parental genomes was known before in the *Ambystoma* complex) and the erection of a new name was required and fully justified. A question arises, however, because *Ambystoma* kl. *nothagenes* populations include both triploid and tetraploid gynogenetic and hybridogenetic individuals, just as *Rana* kl. *esculenta* includes diploid, triploid, and diploid-triploid populations.

I propose that all different ploidy combinations with the same parental genomes be included in the same klepton The main reason is that genetic flow exists between different ploidy forms. For instance diploid *Rana* kl. *esculenta* females in Germany produce both diploid and triploid progeny, thus preventing consideration of diploids and triploids as separate taxa. On the other hand, recent studies of BOGART & LICHT (1986) showed how diploid, triploid, and tetraploid progenies were from the same *Ambystoma* triploid females in Lake Erie. Obviously, separate nomenclature for different ploidy levels would be biologically inacceptable. For these very same reasons I consider *Ambystoma tremblayi* Comeau, 1943 (*Ambystoma 2 laterale-1 jeffersonianum*, sensu SCHULTZ, 1969) a junior synonym of *Ambystoma* kl. *platineum* (Cope, 1867) (*Ambystoma 1 laterale-2 jeffersonianum*, sensu SCHULTZ, 1969) (see Table I).

KLEPTONS TOWARD THE STATUS OF SPECIES

Kleptons become species either when they become genetically autonomous, or when their hybrid origin is concealed, by accumulative mutations (sensu lato). The phenomena could be compared to diploidization of tetraploid new species after entire genome duplication (OHNO, 1970).

As some peripheral subspecies are involved in speciation processes, thus some kleptic populations could be considered in speciation process, too. Such appears to be the case for some *Rana* kl. *esculenta* populations of East Germany. In these populations *esculenta* hybrids seem to be autonomous with respect to the species *Rana ridibunda* (see a review in GRAF & POLLS PELAZ, 1989). I understand these situations as speciation events (or perhaps only attempts), and I propose to consider these cases as examples of " good " species arising from a kleptic origin (fig. 1).

Perhaps speciation events in *Xenopus* (by allopolyploidy, KOBEL & DU PASQUIER, 1986) are analogous to current hybridogenetic processes in *Rana* kl. *esculenta* (see DUBOIS, 1977). As a matter of fact, derivation of new species from hybrid origin really seems to be related to the tetraploid level (MURAMOTO & OHNO, 1968; OHNO, 1970; COMINGS, 1972; BOGART, 1980; FISHER et al., 1980; ALLENDORF & THORGAARD, 1984). Autotetraploids frequently show tetrads in aberrant meiosis, whereas allotetraploids with an equilibrated parental genome hybrid dosage could constitute a double number of bivalents, and " ordinary " meiosis could happen; therefore mixis of diploid gametes could originate a new gonochoric species of tetraploid hybrid origin. Triploids giving diploid gametes could be an intermediate step between kleptons and species in the *Rana* kl. *esculenta* complex.

Source MNHN, Paris

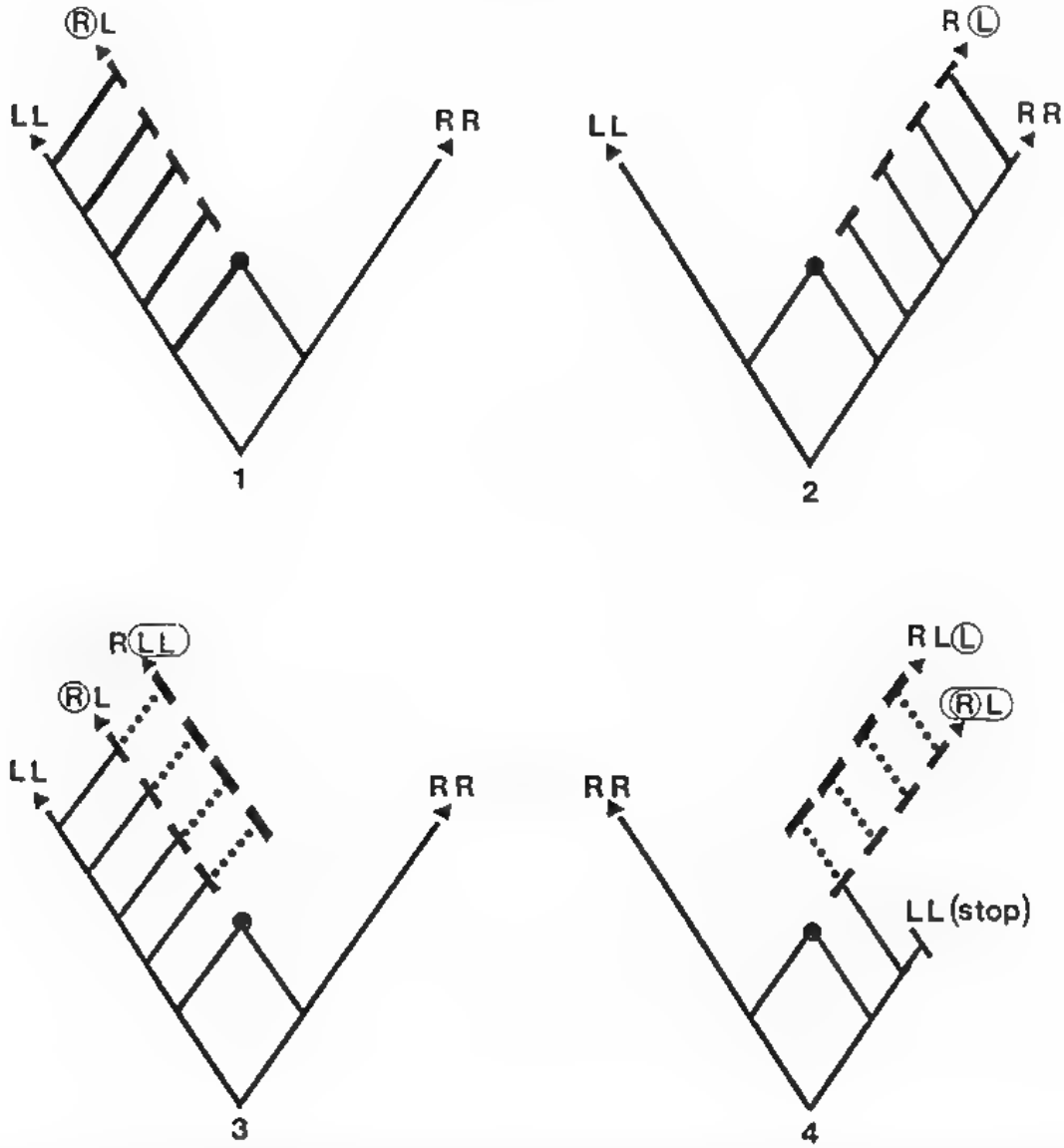

Fig. 1 - Some evolutionary trees illustrating different genetical sytems in the Palearctic populations of *Rana* kl *esculenta* complex: 1 (the so-called L-E system), 2 (the so-called R-E system); 3 (all-male allotriploid genealogies in Fontainebleau forest); and 4 (Serrahn pure *esculenta* populations) Circles indicate hemiclonally transmitted genomes Abbreviations refer to the following genomes: R = *R ridibunda*, L = *R. lessonae*, RL, RLL = *R.* kl. *esculenta*. For more explanations see the review of Graf & Polls Pelaz (1989)

Introgression, mosaicism, and clonal-hemiclonal diversity in kleptons

Kleptons seem to play an important rôle as a genetic vector of introgression both between their associated "good" species, and between other involved klepton. For instance high introgression levels of *Poeciliopsis viriosa* genes into the *monacha* hybrido-

Source MNHN, Paris

genesis-inducer genome have been found in Rio Moccorito's *Poeciliopsis monacha-viriosa* hybrid populations. In those populations recombinant *monacha-viriosa* haploid gametes occur, becoming inductors of hybridogenesis when crossed with sympatric individuals of *Poeciliopsis lucida*. Thus diploids of *Poeciliopsis (monacha-viriosa)-lucida* become separate, hemiclonal hybridogenetic taxa in reproductive dependence on the " good " species *P. lucida* (VRIJENHOEK & SCHULTZ, 1974). This unnamed klepton seems to have evolved as a separate unit, perhaps much closer to the species level than Rio Grande triploid kleptons of trihybrid *monacha-viriosa-lucida* genome dosage. I conclude that high levels of introgression should be reflected with the use of separate names. Low levels of introgression (for instance in some populations of *Rana* kl. *esculenta* complex, see a review in GRAF & POLLS PELAZ, 1989) are irrelevant for consideration of separate taxa.

Mosaicism occurs in *Phoxinus* kleptons (DAWLEY & GODDARD, 1988) as well as in some " good " species (SERRA, 1965), and findings of this kind must not be considered problematic for using kleptic nomenclature for hybrids with hybridogenetic or gynogenetic reproduction.

Hemiclonal and clonal diversities in *Rana* and *Poeciliopsis* kleptons have been reviewed respectively by HOTZ (1983) and VRIJENHOEK (1984). This would constitute a problem for nomenclatural systems based only on genome dosage (because each clone is a " separate ", self-evolving genome). But no problem is encountered in kleptic nomenclature, which provides for different degrees of polymorphism between populations.

KLEPTONS AND EVOLUTION

" The species are the real units of evolution. " (MAYR, 1982: 621).

It could be that all genotypes in tetrapod vertebrate taxa have a common ancestor (500 Myr ago) in which duplication at least once of the entire genome took place (OHNO, 1970). In some cases in entire families, as salmonids (ALLENDORF & THORGAARD, 1984) and catostomids (FERRIS, 1984), as well as at least twelve more fish species (ALLENDORF & THORGAARD, 1984), a trace of " recent " (in catostomids 50 Myr) polyploidization events still remains Polyploid amphibians and reptiles are surprisingly common (DUBOIS, 1977; BOGART, 1980). In some cases, as in the entire genus *Xenopus*, evidence of allopolyploidy remains (KOBEL & DU PASQUIER, 1986). In other case, as for instance in the triploid-tetraploid *Carassius auratus* complex, hybrid origins are likely, because the parental species are allopatric, and divergent evolution of the taxa has taken place (LIEDER, 1955; CHERFAS, 1966; KOBAYASI, 1971; KOBAYASI et al., 1970).

But it is clear that hybridization could be the basis of polyploidy (BOGART & WASSERMAN, 1972; DUBOIS, 1977), perhaps in the way proposed by SCHULTZ (1969), by (1) the origin of a triploid strain (hybridogenetic or gynogenetic, unisexual or not), followed by (2) occasional fertilization of the triploid by normal diploid to produce fertile tetraploids.

Gametogenetic mechanisms are involved. CUELLAR (1987) reviewed all meiosis variants for parthenogenesis (sensu lato, including hybridogenesis and gynogenesis) in plants and animals, in discussing " Spontaneous versus Hybridization controversy " In

Source MNHN, Paris

fact meiotic, premeiotic, and before-meiosis *extravagancies* (Table I) are at the origin of all gynogenetic and hybridogenetic hybrid populations. I conclude that at least some kleptons could be considered as hybrid taxa currently evolving toward the status of polyploid " good " species. The process could be favored by heterosis (BULGER & SCHULTZ, 1979; MOORE 1976, 1984), and hemiclonal-clonal adaptation of hybrids to intermediate environments (THIBAULT, 1978; THIBAULT & SCHULTZ, 1978).

PERSPECTIVE IN THE USE OF KLEPTIC TERMINOLOGY

The history of taxonomy is an evolutionary event, too, and it is not evident whether kleptic nomenclature will be accepted by the international scientific community. Some European authors routinely use this system of nomenclature for the *Rana* kl. *esculenta* complex. The advanced state of knowledge in *Poeciliopsis, Phoxinus* and *Poecilia* complexes seems to be adequate for the full use of kleptic nomenclature, although names are needed for taxa as yet unnamed.

The 1985 *Code* authorizes interpolation as the proposal for interpolation of " kl. " in scientific names – although to be sure in a different context, viz. species-groups and subspecies-groups. The principle is the same, however, if the insertion of " kl. " is proposed (see the *Code*, Art. b, p. 10, H. M. SMITH, in litteris).

Canadian zoologists working on the *Ambystoma* complex seem to be in mutual accord for the use of hyphenated names. Since knowledge of some unnamed *Ambystoma* taxa is still inadequate (for instance we do not know if parthenogenesis occurs, even after recent papers published by BOGART and colleagues), it seems consistently proper to continue to use provisional terms

It was LINNAEUS who first used binomial names for species. But that concept was erected thousands of years earlier by Grecians such as ARISTOTELES. And the BSC needed around two centuries from LINNAEUS to MAYR in order to become formally constituted. The klepton sytematic-evolutionary category was proposed only in 1982 by DUBOIS & GÜNTHER, from which the BKC is available; its fate may require decades to be finalized.

ACKNOWLEDGEMENTS

I thank Dr. Jean-Daniel GRAF for comments on the manuscript, as well as Dr. Alain DUBOIS for discussion of these topics over the last several years I am indebted to Dr. Hobart M. SMITH for his review of my English text

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Source MNHN, Paris

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Corresponding editor: Andrew H. PRICE

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Source MNHN, Paris

Alytes, 1989-1990, **8** (3-4): 90-98.

Mating pattern in pure hybrid populations of water frogs, *Rana* kl. *esculenta* (Anura, Ranidae)*

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The existence of pure hybrid populations is one of the most interesting phenomena within the *Rana* kl. *esculenta* synklepton. The aim of our investigations, carried out on two *esculenta* populations, was to clarify whether particular genotypes are favoured during mating. A comparison between the theoretical frequencies of every mating combination (diploid male × diploid female, diploid male × triploid female, triploid male × diploid female, triploid male × triploid female), calculated on the basis of the population structure, and the observed frequencies yielded no significant differences. This indicates that diploid and triploid individuals have equal chances to mate. Triploid females probably play a secondary role in the population structure as their frequencies amounted to only 5.5 % in the population A and to 6.6 % in the population B. Diploid males were found in a relatively high proportion in the population A (19.5 %), while they amounted to only 6.6 % of individuals in the population B. While in population A the mating combinations, diploid male × diploid female and triploid male × diploid female, had nearly the same frequencies, in population B most matings occurred between triploid males and diploid females.

Moreover, we found no clear evidence for mating choice in relation to body size.

PROBLEM

In Central Europe the hybridogenetic edible frog, *Rana* kl. *esculenta*, mainly lives in populations together with only one of its two parental species, either *Rana lessonae* or *Rana ridibunda*. For its reproduction *esculenta* is fundamentally dependent on these parental forms. Due to their hybridogenetic gamete producing system the hybrids mainly give rise to pure parental gametes, while genetic recombination and introgression occur at a very low level (UZZELL & BERGER, 1975; TUNNER & DOBROWSKY, 1976; UZZELL et al., 1977; GÜNTHER, 1973). Surprisingly, pure hybrid populations exist in several parts of Europe, for example in Germany, Poland, Sweden and probably Denmark (see GUNTHER, 1973, 1974, 1975, 1990; EBENDAL, 1979, EIKHORST, 1984; BERGER, 1988).

In the pure *esculenta* populations it could be shown that a certain number of frogs were triploid (GÜNTHER, 1975). Moreover, by means of morphological, serological and enzymological studies it became evident that these hybrids had two genetic compositions: one with two *lessonae* genomes and one *ridibunda* genome (LLR) and a second with one

* This paper was presented during the symposium on "Modified sexual systems: parthenogenesis and hybridogenesis" convened and moderated by John WRIGHT and Rainer GÜNTHER as part of the First World Congress of Herpetology (University of Kent at Canterbury, United Kingdom, 11-19 September 1989).

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lessonae genome and two *ridibunda* genomes (LRR). The latter are very rare in most hybrid populations in Germany (GÜNTHER, UZZELL & BERGER, 1979; GÜNTHER, 1983; BERGER & GÜNTHER, 1988).

While the reproductive system of mixed populations has been more or less well elucidated, the mechanisms for the maintenance of pure hybrid populations have not yet been clarified in all their details. Considering the joint occurrence of six different genotypes (LR males, LR females, LLR males, LLR females, LRR males, LRR females) theoretically nine different mating combinations may occur. The aim of our study was to clarify whether mating occurs by chance or whether mating preferences between certain genotypes exist. In this context relations between the observed mating frequencies of different genotypes and the genotypic structure of the population are discussed.

Besides, we investigated the significance of body size of water frog males and females for mating choice.

MATERIAL AND METHODS

The study was performed on individuals from two populations: population A was found in an eutrophic garden pool in Berlin, population B lives in a small pond in a meadow near Boltenhagen, at the shore of the Baltic Sea. In both populations only *esculenta* phenotypes were found. In the population A 15 pairs were captured on May 18th, 1988 and 22 additional pairs on May 26th of the same year. In the population B 18 pairs were caught on May 20th, 1975. All pairs were in amplexus.

Besides, in both populations non-paired individuals were collected at random at the same dates (population A: 16 males and 38 females, population B: 16 males and 10 females). Ploidy was determined indirectly by means of cytomorphological parameters (mean length, width and surface of erythrocytes; see GÜNTHER, 1977).

For all individuals the snout-vent-length (s.v.l.), the length of the first toe (d.p.l.) of the metatarsal tubercle (c.int.l) and of the tibia (t.l.), as well as the distance between the nostril and the caudal eye edge (d.n.e.) and the head width (h.w.) were measured. The ratios, s.v.l./c.int.l., d.p.l./c.int.l., t.l./int.l., h.w./c.int.l. and d n.e./c.int.l., constituted the basis for determining genotype together with the cytomorphological parameters

In the analysis of the data the Chi-square test, to test goodness of fit between observed (f_o) and expected frequencies (f_e), was utilized

GENOTYPIC STRUCTURE

The results of the ploidy analysis and sex ratios in populations A an B are summarized in Table I. In both populations the relation of males to females deviates from the expected 1:1 ratio. However, these deviations are not significant (population A: $\chi^2 = 3.78$, d.f. = 1, $p > 0.05$; population B: $\chi^2 = 0.58$, d.f. = 1, $p > 0.05$).

Source MNHN, Paris

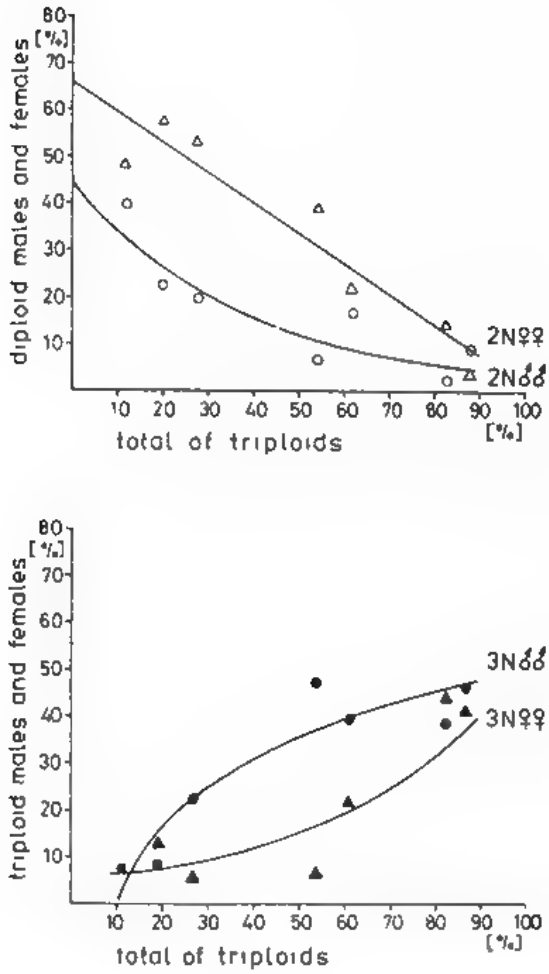

Fig. 1. – Proportion of observed 2N males, 2N males and 3N females in relation to the total of triploids (males + females) in pure *esculenta* populations Data were taken partly from: GÜNTHER, 1975, BERGER, 1988; BERGER & GÜNTHER, 1988. The functions are empirically fitted to the data

Table I. – Proportion of different genotypes in populations A and B (m, males; f, females; 2N, diploid; 3N, triploid).

Sample	n	Proportion of genotypes						Sex ratio
		2N	3N	2N m	2N f	3N m	3N f	m: f
A	128	93 (72.7 %)	35 (27.3 %)	25 (19.5 %)	68 (53.1 %)	28 (21.9 %)	7 (5.5 %)	1. 1.42
B	61	28 (45 9 %)	33 (54.1 %)	4 (6 6 %)	24 (39.3 %)	29 (47.5 %)	4 (6.6 %)	1· 0 82

Source MNHN, Paris

The proportion of triploid individuals in populations A and B are significantly different ($\chi^2 = 12.83$, d.f. = 1, $p > 0.001$). In the population A only 27.3 % triploid individuals were found, while in the population B their frequency was 54.1 %.

While the proportion of triploid females in both populations was quite similar (5.5 and 6.6 %), the high triploid rate in the population B can be attributed to the relatively large number of triploid males (47.5 %).

As fig. 1 shows, in pure *esculenta* populations the proportion of triploid individuals can be due mainly to the high proportion of triploid males. In most *esculenta* populations examined up to now, there exists an excess of males among triploid individuals. Only when

Table II. Morphological parameters of diploid (2N) and triploid (3N) *Rana* kl. *esculenta* from populations A and B in comparison to the same parameters of central European *Rana lessonae* and *Rana ridibunda*. n, number of individuals; s.v.l., snout-vent-length; c.int.l., callus internus length; d.p.l., digitus primus length; t.l., tibia length; h.w., head width; d.n e., eye-nostril distance.

Genotype	n	Ratio sv.l./ c.int.l.	d.p.l./ c.int.l.	t.l./ c.int.l.	h.w./ c.int.l.	d.n.e / c.int.l.
Rana kl. *esculenta*						
Sample A						
2N males	21	13 6-17.5 (15 8 ± 1.10)	1.8-2.5 (2.2 ± 0.19)	6.9-9.0 (7.9 ± 0.60)	5.3-6.7 (5.9 ± 0 41)	2.6-3.5 (3.0 ± 0.22)
2N females	48	14.4-18.6 (16 0 ± 1.13)	1.9-2.7 (2.2 ± 0.18)	6.6-9.4 (7.7 ± 0.60)	4.5-6 8 (5.7 ± 0.52)	2.5-3.5 (2.9 ± 0.24)
3N males	21	13.7-16 5 (15.0 ± 0.78)	1 6-2.2 (2.0 ± 0.16)	6.7-7.8 (7.3 ± 0.37)	5.0-6 1 (5.5 ± 0.26)	2 6-3 2 (2.9 ± 0.16)
3N females	5	15.3-16.1 (15.7 ± 0.35)	1 9-2 2 (2.0 ± 0.10)	7.1-7.8 (7.5 ± 0.24)	5.7-5.8 (5.8 ± 0.04)	2 9-3 0 (2.9 ± 0 04)
Sample B						
2N males	3	15.6-17.4 (16.3 ± 1.0)	2.2-2 4 (2.3 ± 0.10)	7 6-8.3 (7.9 ± 0 35)	5 5-5.8 (5.6 ± 0.18)	2.8-3.0 (2.9 ± 0.1)
2N females	24	15.4-20.2 (17.8 ± 1.24)	2.2-2.9 (2.6 ± 0.19)	7.3-9.3 (8.4 ± 0 52)	5.7-7.2 (6.2 ± 0.37)	2.6-3.6 (3.1 ± 0.22)
3N males	28	14.3-18.0 (16.1 ± 0.94)	2.0-2.4 (2.2 ± 0.13)	6.9-8.3 (7.7 ± 0 36)	5.0-6.4 (5 6 ± 0.32)	2.4-3.4 (3.0 ± 0.20)
3N females	4	16.3-19.5 (17.4 ± 1.52)	2.2-2.5 (3.3 ± 0.20)	7.7-9.0 (8.1 ± 0.60)	5.6-6.5 (6.0 ± 0.36)	2.8-3.5 (3.1 ± 0.28)
Rana lessonae						
	19	10.0-14 3 (12.3 ± 1.17)	1 3-1.7 (1.5 ± 0.10)	5.1-6.7 (5.9 ± 0.41)	3.5-5 3 (4.5 ± 0 45)	2.2-2.8 (2.6 ± 0.18)
Rana ridibunda						
	47	17.4-25.4 (20.7 ± 1.93)	2.3-3.9 (3.0 ± 0.36)	9 2-14.2 (11.1 ± 1.06)	6.3-9 3 (7.6 ± 0.80)	3 1-4.7 (3 8 ± 0.39)

Source MNHN, Paris

the proportion of triploids reaches about 80 % does the ratio 3N males / 3N females seem to become more or less balanced again. Moreover, it is noteworthy that in all populations examined up to now, there was a clear excess of females among the diploid individuals

Morphological parameters of the investigated individuals are given in Table II. In both populations the values of these parameters were slightly lower in the triploid than in the diploid individuals. Compared with the parental species the values of the diploid as well as the triploid individuals were more similar to those of *Rana lessonae*. This fact, the frequency-distribution of the morphological parameter and cluster-analyses, carried out on the basis of these ratios, lead to the assumption, that with one possible exception all triploid individuals possess one *ridibunda* and two *lessonae* chromosome sets (LLR genotype) (PLÖTNER, unpublished). The ratios of one female (No. 45) from population B showed values that are *ridibunda* specific. However, the metatarsal tubercle exhibited a shape typical for diploid *Rana* kl. *esculenta*. Possibly this female was of the genotypic composition LRR.

MATING FREQUENCIES OF INDIVIDUAL GENOTYPES

Due to the existence of four different genotypes: 2N [LR] males, 2N [LR] females, 3N [LLR] males and 3N [LLR] females in both populations, the following four mating combinations can occur:

1. 2N [LR] male × 2N [LR] female
2. 2N [LR] male × 3N [LLR] female
3. 3N [LLR] male × 2N [LR] female
4. 3N [LLR] male × 3N [LRR] female

In order to clarify the question whether certain mating combinations occur more frequently than others, the expected frequencies (f_e) of individual combinations must first be calculated on the basis of the genotypic structure of each population. As the proportion of each genotype was estimated from a random sample, f_e only represents an approximate value. f_e was calculated according to the formula:

$$f_e = \frac{n_{mj}}{n_m} \quad \frac{n_{fi}}{n_f} \quad n_p \qquad \text{where}$$

n_{mj} = number of male genotypes of the corresponding combination,
n_{fi} = number of female genotypes of the corresponding combination,
n_m = total of males in the mated and unmated subsample,
n_f = total of females in the mated and unmated subsample,
n_p = total of pairs captured in the population.

Table III shows the expected and observed frequencies of all mating combinations The differences between the observed and expected frequencies are not statistically significant, neither in population A ($\chi^2 = 0.94$, d.f = 3, $p > 0.05$) nor in population B ($\chi^2 = 3.85$, d f. = 3, $p > 0.05$).

Source MNHN, Paris

Table III. – Observed (f_o) and expected (f_e) frequencies of all possible mating combinations in populations A and B (m, male; f, female, 2N, diploid; 3N, triploid).

Combination m × f	Population A Observed frequency f_o	n_p = 37 Expected frequency f_e	Population B Observed frequency f_o	n_p = 18 Expected frequency f_e
2N × 2N	18	15.825	1	1.868
2N × 3N	1	1 628	0	0 311
3N × 2N	17	17.723	17	13 558
3N × 3N	1	1 824	0	2.259

In order to test whether the carriers of certain genotypes exhibit mating preferences, the frequencies of genotypes in paired and single adults were compared (Table IV). While in population A no significant deviations were found between the observed and the expected frequencies (χ^2 = 7.46, d.f. = 3, $p > 0.05$), in population B these differences were significant at a 5 % level (χ^2 = 10.21, d.f. = 3). This latter fact depends mainly on a greater number of observed 2N mated females than was theoretically expected. However, as the sample size in population B was relatively small, this result should be viewed cautiously. It can therefore be concluded that, in principle, all the genotypes possess equal mating chances.

Table IV. – Observed (f_o) and expected (f_e) frequencies for mated and unmated individuals of different genotypes in samples A and B (2N, diploid; 3N, triploid).

Genotype	Sample A				Sample B			
	Mated individuals		Unmated individuals		Mated individuals		Unmated individuals	
	f_o	f_e	f_o	f_e	f_o	f_e	f_o	f_e
2N male	19	14.45	6	10.55	1	2 36	3	1.64
2N female	35	39.31	33	28.69	18	14.16	6	9 84
3N male	18	16 19	10	11 81	17	17.11	12	11 89
3N female	2	4.05	5	2.95	0	2.36	4	1.64

In *esculenta* populations, LR males normally form haploid R gametes while LR females can produce haploid R as well as diploid LR gametes Triploid individuals of LLR genotype mainly form gametes with one *lessonae* genome and triploid ones of LRR genotype mainly form gametes with one *ridibunda* genome (see GÜNTHER, UZZELL & BERGER, 1979; GÜNTHER, 1983; BERGER & GÜNTHER, 1988).

The hypothesis sustained up to now that the structure and stability of *esculenta* populations is based mainly on crosses between triploid males and diploid females (see GÜNTHER, UZZELL & BERGER, 1979; GÜNTHER, 1988) seems to be valid only for such populations in which the proportion of triploids lies between 30 and 70 %. From such crosses diploid LR and triploid LLR individuals can originate. In populations consisting

Source MNHN, Paris

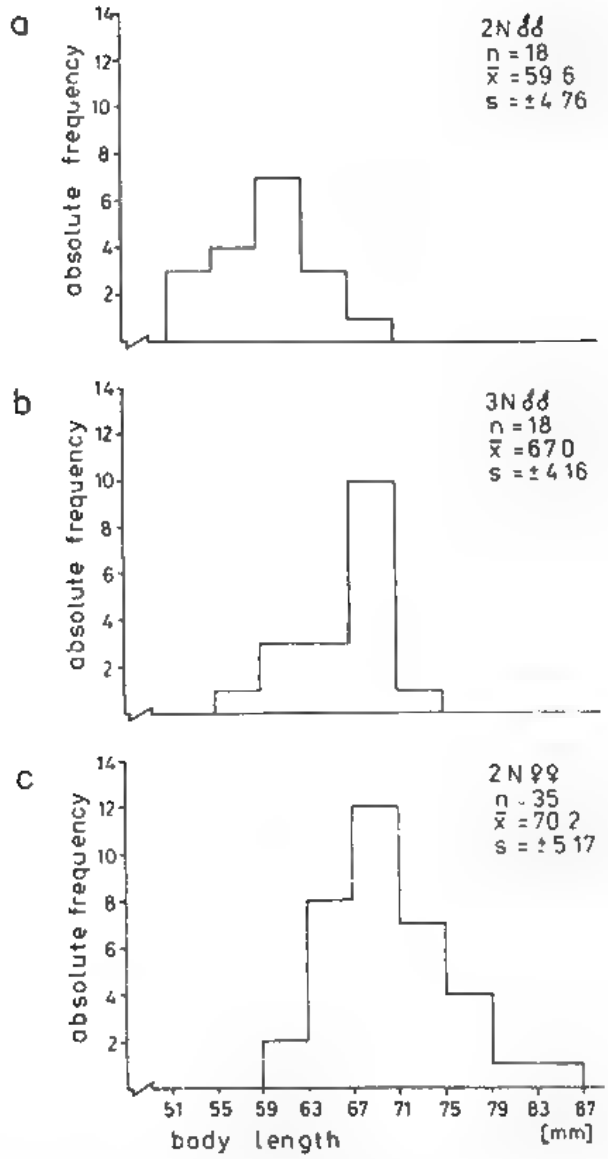

Fig. 2. Distribution of body length in members of pairs captured in amplexus in population A
a: 18 diploid males (combination 2N male × 2N female and 2N male × 3N females);
b: 18 triploid males (combination 3N male × 2N female and 3N male × 3N female);
c: 35 diploid females (combination 2N male × 2N female and 3N male × 2N female)

mainly of diploid individuals, most crosses should correspond to the combination 2N male × 2N female, while in those populations with a high proportion of triploids, the combination 3N male × 3N female should prevail (see fig. 1).

In most *esculenta* populations from Germany, the majority of triploid individuals are of LLR genotype and form gametes with one *lessonae* genome (see GÜNTHER, UZZELL & BERGER, 1979, GÜNTHER, 1983; BERGER & GÜNTHER, 1988). From crosses between two

Source MNHN, Paris

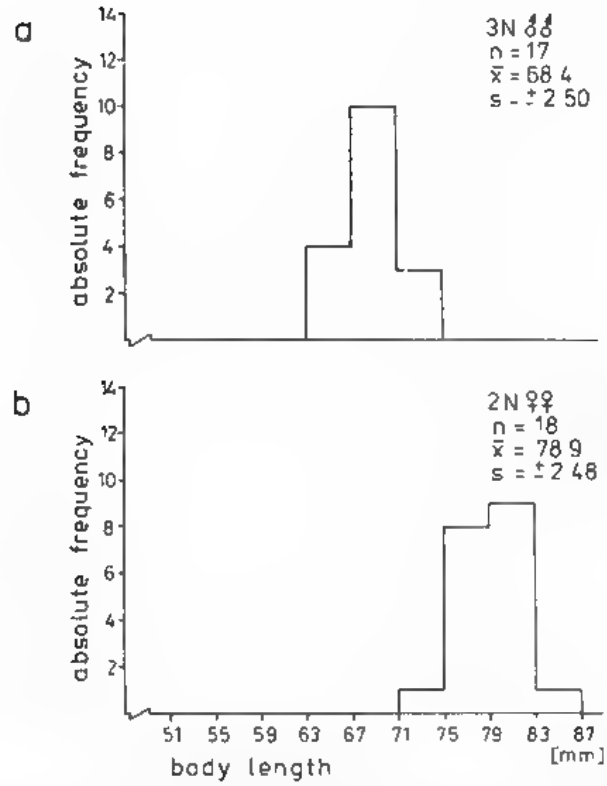

Fig. 3. Distribution of body length in members of pairs captured in amplexus in population B. a: 17 triploid males (combination 3N male × 2N female); b: 18 diploid females (combination 2N male × 2N female and 3 male × 2N female).

LLR individuals mainly *lessonae* (LL) genotypes result. It is known that these, just as the RR genotypes from LR × LR crosses, do not survive in *esculenta* populations. It follows that in *esculenta* populations with an increasing proportion of triploid individuals, either the rate of reproduction decreases and the population reaches an "end stage", or the LLR females must form, besides haploid L gametes, a certain number of diploid LR ones (see GÜNTHER, UZZELL & BERGER, 1979; GÜNTHER, 1983).

BODY SIZE OF MATING PARTNERS

In the mean, females in population A were 11 % and in population B, about 14 % larger than their male partners. The greatest difference (31 %) between the body length of a female (74 mm) and that of its male (51 mm) partner was found in population A in a pair of the 2N male × 2N female combination. The reverse situation also appeared in population A, in a combination 3N male × 2N female. Here the body length of the male

Source MNHN, Paris

was 70 mm, that of the female, 62 mm; this corresponds to a difference of 11 % in favour of the male

Among the 55 pairs captured in amplexus the male was larger than the female in only four pairs (7.3 %) although, according to the distribution of body length (fig. 2a-c, 3a and b) at least in the population A, a higher proportion could have been possible. While in population B all the diploid females of the pairs were larger than the triploid males, in population A there was an overlap between the distribution of body length of the male and female partners. Although males seem to prefer larger to smaller females there is no clear evidence for significant size related mating preferences.

How mating choice takes place in European water frogs has not yet been clarified in detail.

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Corresponding editor: Alain DUBOIS.

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Source MNHN, Paris

Alytes, 1989-1990, **8** (3-4): 99-104.

Images d'Amphibiens camerounais. II. L'enfouissement et la phonation bouche ouverte chez *Conraua crassipes* (Buchholz & Peters, 1875)

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Four photos of the ranid *Conraua crassipes* taken in Cameroon are commented upon. They show the burying behaviour of the species, already described by Knoepffler (1965), and the emission of calls, whistlings which are produced with the mouth half-opened. Until now, phonation with the mouth opened was known in anurans only for distress calls, but not for nuptial calls.

Avec ses 8 cm de taille maximale, *Conraua crassipes* paraît bien modeste à côté de ses deux autres congénères camerounaises, *C. robusta* (15 cm) et *C goliath* (30 cm). Un habitus assez banal, une livrée terne variant du jaunâtre au brunâtre (fig. 1) et des mœurs discrètes n'en font pas, a priori, un sujet d'étude très attractif pour le batrachologue séjournant au Cameroun, où bien d'autres espèces sortant de l'ordinaire peuvent solliciter son attention.

La distribution géographique de *C. crassipes* n'offre pas non plus de motif d'intérêt particulier: l'espèce est largement répandue dans l'Afrique centrale forestière, depuis le Nigéria jusqu'à l'ouest de la cuvette congolaise. Au Cameroun, sa présence peut être décelée dans la plupart des petits cours d'eau permanents, pourvu qu'ils coulent en sous-bois sur un fond de sable ou de gravier, au moins par endroits, et que l'eau y soit limpide et bien aérée.

Observée dans son milieu, cette grenouille à première vue anodine a pourtant révélé des particularités comportementales qui la distinguent des autres Batraciens camerounais et même, sur un point, de l'ensemble des Anoures.

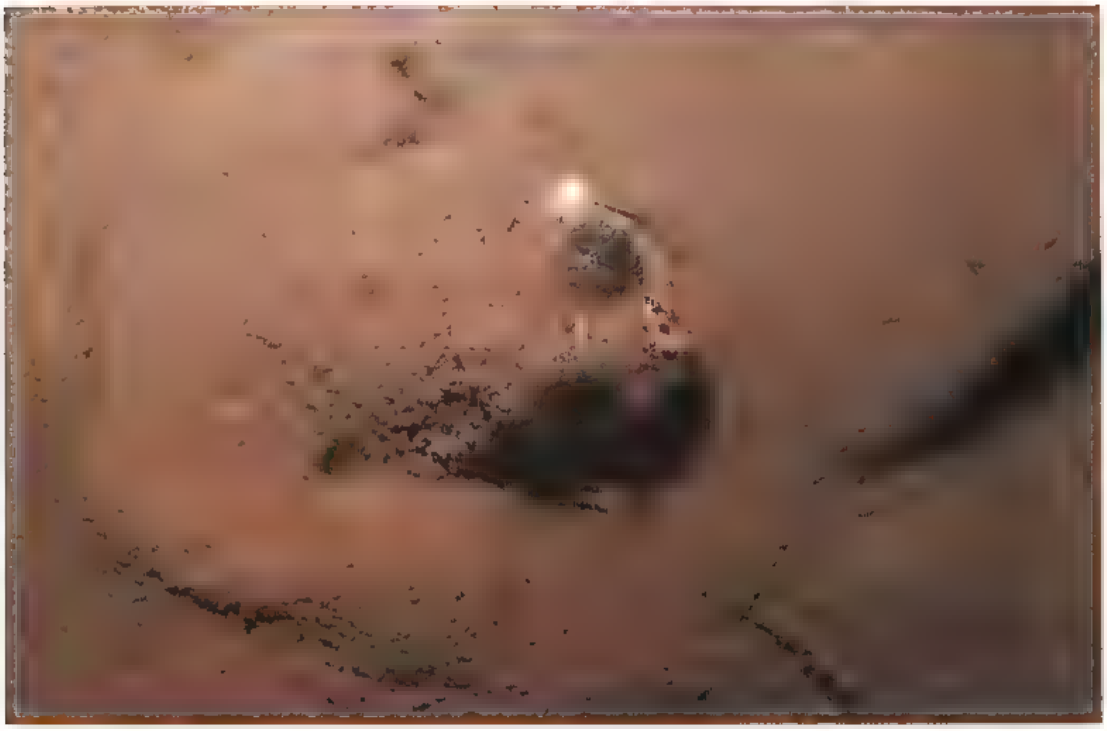
Le comportement d'enfouissement

Une première contribution à la connaissance de l'éthologie de *C. crassipes* a été fournie par Knoepffler (1965).

Cet auteur a décrit en particulier, à partir d'observations faites à Makokou (Gabon), le comportement d'enfouissement de cette espèce: effrayée, *C. crassipes* saute à l'eau mais, au lieu de se blottir sur le fond, s'enfouit en un clin d'œil dans le sable, le gravillon ou le limon qui le tapisse. Ce comportement permet à l'animal de se dissimuler dans des cours

Source MNHN, Paris

1

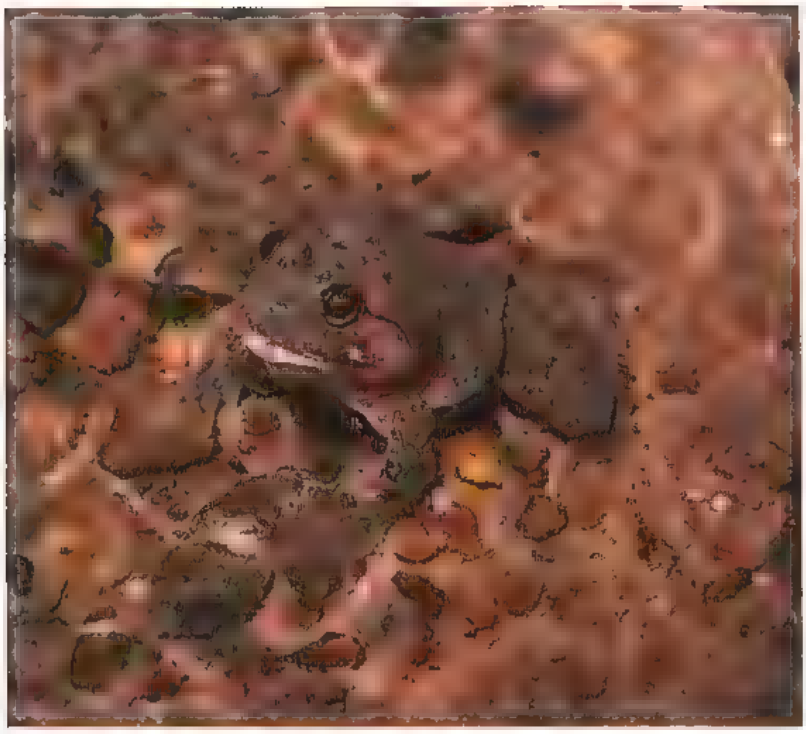


2

Fig 1. *Conraua crassipes*, Kala, 19-IX-80. Sur la cuisse et la jambe les fins plis cutanés caractéristiques des *Conraua* sont bien visibles. Comme il arrive fréquemment, un Diptère hématophage se nourrit sur le dos de l'animal qui ne paraît pas importuné par la piqûre.

Fig 2. *Conraua crassipes*, Kala, 16-VII-79. Après s'être enfouie, la grenouille s'apprête à sortir et pointe le museau hors du sable.

Source MNHN, Paris



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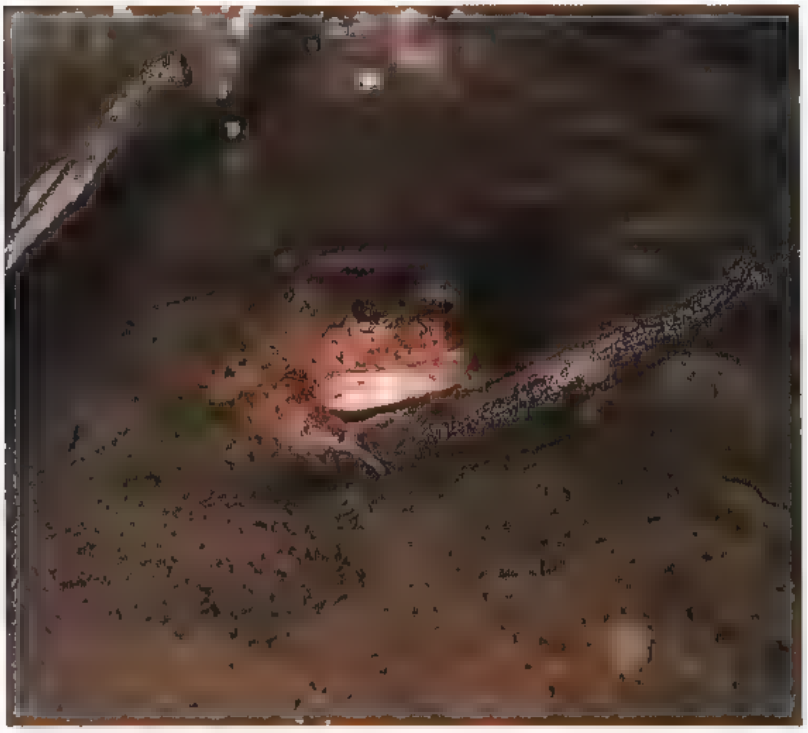

4

Fig 3 *Conraua crassipes*, Kala, 6 XII-76. Mâle photographié juste au moment où il émet son sifflement, en appui sur les membres antérieurs et l'arrière-corps immergé La production du son n'est précédée que d'un faible gonflement du corps L'animal est en butte aux attaques de plusieurs Diptères piqueurs concentrés sur les parties émergées

Fig. 4. *Conraua crassipes*, Kala, 2-II-77. Mieux que le précédent, ce cliché permet d'observer les deux excroissances de la mâchoire inférieure et l'espace qui les sépare

Source MNHN, Paris

d'eau dont la faible profondeur (quelques centimètres) et l'habituelle limpidité ne sauraient le soustraire à la vue d'un prédateur. Les mouvements d'enfouissements sont analysés et illustrés de plusieurs photos dans l'article de KNOEPFFLER (1965) auquel je renvoie le lecteur désirant plus de précisions[1].

L'alerte passée, la grenouille, qui n'était recouverte que par une mince couche de sédiment, s'échappe prestement après avoir d'abord fait pointer son museau: c'est cet instant de la sortie qu'a fixé la photo de la figure 2.

Au Gabon, KNOEPFFLER (1965) a d'autre part remarqué que, pendant la nuit, *C crassipes* se tient souvent au sommet d'une accumulation de sable tronconique, affleurant à la surface de l'eau et haute d'une dizaine de centimètres au plus, d'où elle peut s'élancer pour capturer une proie. Je n'ai jamais observé de telles constructions au Cameroun, probablement parce que les caractéristiques granulométriques et mécaniques des substrats ne s'y prêtent pas. KNOEPFFLER (1965) rapporte d'ailleurs que les spécimens qu'il avait ramenés en France n'ont pas construit d'édifice, ce qu'il attribue à la nature du sable mis à leur disposition et le conduit à estimer qu'"il ne s'agit pas d'édification volontaire".

A ma connaissance, l'enfouissement immédiat et systématique dans le fond meuble des cours d'eau, tel que le pratique *C. crassipes*, n'existe pas chez d'autres espèces d'Anoures camerounais, y compris chez ses deux proches parentes *C. robusta* et *C. goliath*.

C. crassipes, comme on va le voir, ne se singularise pas seulement de cette façon.

LES VOCALISATIONS ET LEUR MODE D'ÉMISSION

Les appels de *C. crassipes* sont des sifflements brefs, puissants, généralement redoublés et d'une tonalité très pure. Le plus souvent, ils sont séparés par des intervalles atteignant la minute, mais ils peuvent se succéder plus rapidement si un autre individu se trouve dans les parages. Les mâles sifflent le long de petites rivières ou de ruisseaux, souvent sur des bancs de sable ou de gravier entourés d'eau peu profonde, et toujours en sous-bois. L'activité vocale, dans le cycle circadien, débute au lever du jour puis décline rapidement; durant la journée, il n'y a que de brèves phases d'émission ou des sifflements isolés; l'activité connaît un second maximum avant la tombée de la nuit, vers 18 h. Le plus souvent, les mâles sont très dispersés, distants de plusieurs mètres ou dizaines de mètres, mais lorsque le site et le moment sont favorables, ils peuvent être plus rapprochés: à l'aube et au crépuscule les sifflements se succèdent alors sans relâche, mais ces phases d'excitation vocale durent peu. Au Cameroun, *C. crassipes* se fait entendre surtout en début et fin de grande saison sèche (décembre-janvier, mars-avril) et en petite saison sèche (juillet).

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1 *C crassipes* ne montre aucun caractère adaptatif en rapport avec ce comportement d'enfouissement, qu'il vaudrait mieux ne pas confondre avec le comportement fouisseur pratiqué en milieu terrestre, surtout dans les régions à substrat meuble, par d'assez nombreuses espèces d'Anoures

Source MNHN, Paris

La qualité acoustique des cris de *C. crassipes* est bien plus avienne qu'amphibienne et l'origine des appels est très difficile à localiser. Je ne me sens donc pas gêné d'avouer qu'il m'a fallu plus d'un an après le début de mes recherches batrachologiques au Cameroun pour acquérir la conviction que les doubles coups de sifflet que j'entendais si souvent en forêt, invariablement émis près d'un petit cours d'eau, ne pouvaient provenir que de *C crassipes*. Mais il ne s'agissait encore que d'une conviction et c'est seulement deux ans plus tard (précisément le 14 décembre 1973, lors de ma 305ème sortie de nuit) que je pus voir au crépuscule un mâle moins craintif que les autres ou peut-être plus motivé par la proximité d'un rival ! – en train d'émettre ses sifflements. L'animal fut alors observé de dessus, précision qui, on le verra, a son importance...

Au moment où ma présomption se trouvait ainsi confirmée je ne me doutais pas que, à quelques centaines de kilomètres de là, au Gabon, d'autres chercheurs étaient tenus en échec par ce mystérieux siffleur. Dans son ouvrage *La vie dans la forêt équatoriale*, BROSSET (1976) relate de façon très vivante ses tentatives infructueuses d'identification: "Lors de mes premières prospections en forêt gabonaise, j'avais été frappé par un sifflement mélancolique et pur, souvent entendu au bord des marigots dans les parties les plus sombres du sous-bois. L'auteur me parut en être un Oiseau, et j'essayai de découvrir l'identité de ce chanteur remarquable. Tous mes efforts furent vains; l'animal, excessivement farouche et doué d'une étonnante acuité visuelle ou auditive, détectait les approches les plus précautionneuses, de longs affûts immobiles, près du repaire du chanteur, ne me permirent ni de le voir à l'œuvre, ni de reconnaître son espèce. J'interrogeai un chasseur qui, ayant écouté, déclara péremptoire: 'C'est le Crabe' ...".

C'est grâce à un enregistrement sonore réalisé à Makokou que me fit entendre un autre ornithologue, C. CHAPPUIS, que je pus fournir aux collègues du Gabon la solution de l'énigme

Les appels de *C crassipes* sont a priori si peu imputables à un Amphibien que des batrachologues aussi chevronnés que PERRET et KNOEPFFLER sont bien excusables de l'avoir créditée de vocalisations plus en rapport avec les usages vocaux des Anoures du crû pour le premier en effet le mâle "peut... émettre des sons ventriloques" (PERRET, 1966) tandis que pour le second "le chant nuptial... est un grognement peu intense répété plusieurs fois" (KNOEPFFLER, 1965).

Je ne pensais pas, en élucidant l'énigme du cri de *C. crassipes*, que les vocalisations de cette grenouille me réservaient encore une surprise

Le 4 décembre 1975, soit deux ans après avoir vu siffler un mâle pour la première fois, j'eus la possibilité d'en observer un autre se livrant à la même activité mais, cette fois, de profil. J'eus alors l'étonnement de constater que les sons étaient émis *la bouche ouverte*. Cette observation put ensuite être répétée plusieurs fois sur des sujets différents.

C. crassipes se révèle ainsi décidément non conformiste car, chez tous les autres Anoures, les vocalisations sont produites (sauf les cris de détresse) avec la bouche fermée.

Les clichés des fig. 3 et 4 illustrent cette trouvaille inattendue. Pris juste au moment de l'émission du sifflement, ils montrent que la bouche n'est pas largement béante mais entrouverte, ce qui permet de distinguer (fig. 4) les deux protubérances dentiformes portées par la mandibule.

Source MNHN, Paris

Le processus de production des sons utilisé par *C. crassipes* reste à élucider, ce qui ne sera peut-être pas facile. Il faudrait de plus savoir si les autres *Conraua* émettent leurs appels de la même façon: à en juger par leur qualité acoustique chez les espèces dont les vocalisations sont connues (*C. alleni, C. derooi, C. robusta*), il est probable qu'elles procèdent comme *C. crassipes*.

Le cas de *C. crassipes* illustre une démarche apparemment paradoxale de l'évolution: l'abandon d'une méthode de phonation éprouvée, dont l'efficacité est démontrée par la quasi totalité des Anoures, au profit d'une méthode nouvelle, toute différente, mais dont le résultat est le même. Il est peu concevable en effet que la lignée des *Conraua* ait retenu à elle seule un mode de phonation primitif des Anoures ni que, ses ancêtres ayant de tout temps été muets, elle ait adopté, parallèlement à l'ensemble des autres Anoures, un procédé de phonation différent. On doit plutôt supposer que le mode d'émission bouche ouverte s'est développé dans une lignée qui avait auparavant perdu la capacité d'émettre des sons par la méthode habituelle des Anoures, ce dont quelques espèces muettes nous fournissent des exemples dans la faune actuelle.

Le sifflement de *C. crassipes* témoignerait ainsi d'un "repentir de l'évolution" assez comparable aux branchies secondaires relayant les cténidies chez les Nudibranches, à la pseudoconque suppléant à la disparition de la coquille primitive chez les Ptéropodes du genre *Cymbulia*, ou encore aux voies d'accouplement inhabituelles se substituant, chez certaines Punaises, à un orifice génital dont se satisfont des centaines de milliers d'autres espèces d'Insectes !

Résumé

Quatre photos de *Conraua crassipes* (Ranidae) prises au Cameroun sont commentées. Ces photos montrent le comportement d'enfouissement de l'espèce, déjà décrit par Knoepffler (1965), et l'émission des appels, sifflements produits la bouche entrouverte. Jusqu'ici, la phonation bouche ouverte était connue chez les Anoures pour les cris de détresse, mais non pour les appels nuptiaux.

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Corresponding editor: Alain Dubois.

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Source MNHN, Paris

Alytes, 1989-1990, **8** (3-4): 105-106.

Information complémentaire sur les *Telmatobius* (Leptodactylidae) de El Moreno (Jujuy, Argentine)

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Argentinian populations of *Telmatobius* established at El Moreno (Jujuy), originally considered as *T. jelskii* (sensu ANDERSSON, 1906, non PETERS, 1875), actually belong to *T. platycephalus* Lavilla & Laurent, 1989. Information concerning the nomenclatorial history of the species and a chreso-synonymy are also presented.

La chronologie des contributions à la connaissance des deux espèces sympatriques du genre *Telmatobius* vivant à el Moreno s'établit comme suit:

(1) ANDERSSON (1906) attribue à *Telmatobius jelskii* Peters, 1875 le matériel récolté à El Moreno par l'expédition d'Erland NORDENSKIÖLD (1901-1902)

(2) BARBOUR & NOBLE (1920), sans avoir vu les spécimens, estiment cette identification peu probable, étant donnée la distance considérable entre El Moreno et le Département de Junin (Pérou) d'où proviennent les types de *Telmatobius jelskii*, et croient bon d'attribuer les spécimens de El Moreno plutôt à *Telmatobius hauthali* Koslowski, 1895, décrit de la Province de Catamarca (Argentine), beaucoup moins éloignée.

(3) CEI (1980), pour des raisons similaires, les rapporte à *Telmatobius marmoratus* Duméril & Bibron, 1841, espèce effectivement citée par GALLARDO (1961) de la Province de Jujuy (Argentine).

(4) LAVILLA & LAURENT (1989), ayant obtenu des exemplaires de El Moreno, distinguent parmi eux deux espèces nouvelles vivant en sympatrie. *Telmatobius platycephalus* et *Telmatobius hypselocephalus*, toujours sans avoir vu les spécimens étudiés par ANDERSSON.

(5) Cette série fut originellement déposée à la Stockholm Hogskola, institution qui n'existe plus aujourd'hui. Après de laborieuses recherches, elle fut retrouvée au Musée de Stockholm (Naturhistoriska Rijkmuseet). Elle consiste en 4 adultes (NRM NNN 1901428.3139) et 8 larves (NRM NNN 1901428.4139). Les caractères diagnostiques coïncident avec ceux que LAVILLA & LAURENT (1989) ont décrits pour *T. platycephalus*, en particulier ceux qui distinguent cette espèce de *T. hypselocephalus* qui vit en sympatrie avec elle. Les larves n'ont pu être identifiées, parce qu'elles n'ont pas encore été décrites, lacune que le matériel de NORDENSKIÖLD ne permet pas de combler, faute de comprendre une série complète de développement.

Source MNHN, Paris

La chréso-synonymie (SMITH & SMITH, 1972) de *T. platycephalus* doit donc s'établir comme suit:

Telmatobius platycephalus Lavilla & Laurent, 1989

1906. *Telmatobius jelskii* (non Peters, 1875): ANDERSSON, 1906: 4.
1920. *Telmatobius hauthali* (non Koslowsky, 1895): BARBOUR & NOBLE, 1920: 410.
1980. *Telmatobius marmoratus* (non Duméril & Bibron, 1841): CEI, 1980: 255 [part.].
1989. *Telmatobius platycephalus* Lavilla & Laurent, 1989. 78.

REMERCIEMENTS

C'est grâce à l'amabilité de plusieurs personnes que nous avons pu examiner le matériel d'ANDERSSON. En tout premier lieu, Andrew SPARE, consul de Suède à Tucumán, nous a mis en relation avec le personnel de l'Ambassade de Suède à Buenos Aires, lequel nous orienta vers le Musée d'Histoire Naturelle de Stockholm, et le Dr. Erik AHLANDER rechercha pour nous le matériel en question, le trouva et voulut bien nous le confier.

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Corresponding editor: Alain DUBOIS

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Source: MNHN, Paris

Alytes, 1989-1990, **8** (3-4): 107-120.

Miscellanea nomenclatorica batrachologica (XVIII)

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The generic name *Siren* and the specific name *Siren lacertina* are traditionally credited to LINNÉ (1766 or 1767). It is shown here that these names were first published by LINNÉ's student ÖSTERDAM (1766), who is therefore their author, in the nomenclatural sense of the term. The chronology of the first scientific publications dealing with this strange animal is discussed.

INTRODUCTION

La famille nord-américaine des Sirenidae Gray, 1825 a récemment attiré l'attention de plusieurs batrachologues. en effet, en dépit de travaux répétés, la position phylogénétique de ce groupe au sein des Urodèles est encore fort problématique et discutée (DUELLMAN & TRUEB, 1986; LAURENT, 1986)

Le genre-type de cette famille, *Siren*, qui comporte deux espèces, est connu des scientifiques depuis 1766. Tous les auteurs actuels (p. ex · MARTOF, 1973, 1974; FROST, 1985) attribuent le nom générique *Siren* et le nom spécifique *Siren lacertina* à LINNÉ (1766 ou 1767 selon les auteurs) Or il s'avère que l'histoire de ces noms est plus complexe qu'il n'y paraît et que la paternité, au sens nomenclatural, de ces noms, ne doit pas être attribuée à LINNÉ — même s'il fut probablement l'auteur, au sens trivial, de ces derniers Il a donc paru utile de retracer ici de manière quelque peu détaillée l'histoire de la découverte de cet animal étrange et de son entrée dans le monde de la classification et de la nomenclature zoologiques.

LINNÉ (1766, 1767)

MARTOF (1973, 1974) et BRAME (*in* FROST, 1985 618) attribuent les noms *Siren* et *Siren lacertina* à LINNÉ dans l'addenda non paginé qui figure à la fin du Tomus I, Pars II, de la douzième édition du *Systema Naturae*. Or le volume en question est paru en 1767, et non pas, comme ils l'écrivent, en 1766. Par ailleurs, dans cet addenda, LINNÉ (1767: [xxxvi]) fait référence à deux autres mentions antérieures de ces noms, comme suit "de qua

Source MNHN, Paris

pag. 371. lin. ult. & Dissert. *Siren*. Upsal. 1766 c fig.". Il indique que l'espèce a été découverte en Caroline par GARDEN.

Comme l'a noté par exemple BROWN (1908· 127), le nom *Siren lacertina* apparaît en effet, associé à une courte caractérisation, en note infrapaginale en bas de la page 371 du Tomus I, Pars I, de la douzième édition, volume qui est bien paru, lui, en 1766. Dans cette note, LINNÉ fait déja mention ("conf. diss nostr. de Sirene 1766") de la "dissertation" également citée en 1767, qui était donc parue avant ce Tomus I, Pars I.

Dans ces deux brefs textes, LINNÉ (1766, 1767) reste indécis quant à la nature réelle de cet animal: adulte d'une espèce et d'un genre nouveau, ou larve d'une espèce de *Lacerta* (genre dans lequel LINNÉ incluait les Urodèles)? En 1767 toutefois, il estime manifestement avoir plus probablement affaire à l'adulte d'un animal d'un type complètement nouveau, pour lequel il propose l'emploi formel, non seulement d'un nom générique et d'un nom spécifique distincts, mais encore d'un nouveau nom d'ordre, celui des Meantes Cet ordre viendrait s'ajouter, au sein de sa classe des Amphibia, à ceux des Reptiles, des Serpentes et des Nantes. Le nom de *Siren* qu'il adopte pour cet animal évoque manifestement les caractères qu'il lui prête (deux mains pourvues d'ongles et une voix chantante), comme le notent DUMÉRIL, BIBRON & DUMÉRIL (1854: 192): "Pour le désigner, il emprunta à la Mythologie ce nom de Sirène voulant indiquer un être à deux mains, avec une queue de poisson, produisant, comme on le lui avait annoncé, une sorte de voix ou de chant." Après avoir été tournées en ridicule par plusieurs auteurs, les observations de GARDEN sur lesquelles s'appuyaient ces remarques ont du reste été confirmées· il est vrai que les deux espèces actuellement reconnues dans le genre *Siren* peuvent produire des sons, qui ressemblent même parfois à des chants lointains de Rainettes *Hyla cinerea* (CARR, 1940; MASLIN, 1950; NEILL, 1952; GEHLBACH & WALKER, 1970).

ÖSTERDAM (1766, 1769, 1789)

A l'exception de quelques-uns (p. ex.. SCHNEIDER, 1799. 48, DAUDIN, 1803: 272; MERREM, 1820. 188; HOLBROOK, 1842. 102; DUMÉRIL, BIBRON & DUMÉRIL, 1854· 192-193), la plupart des auteurs postérieurs à LINNÉ ont ignoré la "dissertation" (thèse) à laquelle celui-ci faisait allusion Celle-ci a bel et bien été publiée, une première fois avant les textes de LINNÉ qui en font mention, puis de nouveau deux fois après· il en existe trois versions distinctes au Muséum national d'Histoire naturelle de Paris.

Cette thèse fut soutenue à Uppsala (Suède) le 21 juin 1766 par Abrahamus (Abraham) ÖSTERDAM ou OESTERDAM. La première version (ÖSTERDAM, 1766; fig. 1-2) est datée de 1766 et fut manifestement publiée peu après la soutenance. La deuxième version (ÖSTERDAM, 1769) figure dans un recueil de thèses soutenues sous la présidence de LINNÉ, publié en 1769. Le texte en diffère en plusieurs endroits du texte original de 1766. La troisième version (OESTERDAM, 1789), identique à la deuxième, figure dans la deuxième édition du même recueil, publiée en 1789.

Après une longue introduction, ÖSTERDAM (1766, 1769, 1789) fait mention d'un animal étrange, récemment envoyé de Caroline par GARDEN, et dont il donne une

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description très détaillée, ainsi qu'un dessin (fig 2-3)[1] Il rapporte que, selon GARDEN, cet animal vit dans les marais de la Caroline du sud, et que lorsque ces marais s'assèchent cet animal chante d'une voix plaintive, presque semblable à celle des jeunes canards mais plus aigüe et plus claire ("cum exsiccantur paludes, ubi hospitatur, (...), canit voce querula, anatum juniorum fere simile, sed acuta magis atque clara"; ÖSTERDAM, 1766· 12) Pour finir, ÖSTERDAM développe des considérations sur la place de cet animal dans le "Système" de son Maître LINNÉ. Dans le texte de 1766, après de longues hésitations quant à la nature réelle de cet animal (adulte ou larve?) et d'intéressantes remarques sur les phénomènes biologiques de la vie larvaire, de la métamorphose et de la néoténie, ÖSTERDAM (1766. 15) propose le nom générique *Siren* et le nom spécifique *lacertina* pour cet animal; il ajoute que si cet animal s'avérait ne pas être une larve, il faudrait créer pour lui un nouvel ordre, au sein de la classe des Amphibia de LINNÉ, mais ne propose pas de nom pour cet ordre

Dans la planche jointe au texte original de 1766 (fig. 2), ÖSTERDAM figure non seulement l'espèce *Siren lacertina* décrite dans le texte, mais également une autre espèce, *Siren bartholini*. Ce nom latin n'apparaît pas tel quel dans le texte, mais renvoie sans aucun doute à l'animal décrit et figuré par BARTHOLIN (1654 a: 162-166; 1654 b: 169-173, 1654 c: 186-191), dans un ouvrage auquel ÖSTERDAM (1766· 4; 1769· 314; 1789: 314) fait expressément référence. Cet animal, qui pour ÖSTERDAM correspond manifestement à la sirène de la mythologie, avait été récolté dans la "mer du Brésil", disséqué par P. PAVIUS (P. PAW), de Leiden, et figuré (fig. 4): il s'agit très vraisemblablement d'un Lamantin (genre *Trichechus*).

Dans le texte publié en recueil, ÖSTERDAM (1769: 325; 1789: 325) va plus loin. Il reconnaît formellement un ordre des Meantes, avec un seul genre, *Siren*. Si dans le texte il ne mentionne que l'espèce nominale *Siren lacertina*, en revanche sur la planche (fig 3) et également dans la légende de celle-ci figurent les deux noms *Siren lacertina* et *Siren bartholini*; dans la légende de la planche, cette dernière espèce est toutefois présentée comme "peut-être inventée" ("forte ficta"). Il est donc clair qu'ÖSTERDAM avait quelques doutes sur l'existence de cet animal marin, mais aucune certitude à cet égard. dans le doute, il préférait reproduire la figure que BARTHOLIN (1654 a. 164; 1654 b. 171, 1654 c: 189) en avait donnée, renvoyer à la description de cet auteur, et donner un nom latin formel à cette espèce, qu'il plaçait dans le même genre nominal que l'animal de Caroline qu'il avait sous les yeux.

ELLIS (1767)

Une remarque intéressante figure après le nom de *Siren lacertina* à la fin du texte d'ÖSTERDAM publié en recueil· "Hujus, post hoc editum opusculum, novam historiam, cum optima figura, edidit acutissimus D. Ellis in Act. angl vol 56 p. 189 t. 9." ("De celle-ci,

1 La planche reproduite ici en fig. 2 est tirée d'un exemplaire de l'édition originale de 1766 qui se trouve à la Bibliotheque Nationale de Paris L'exemplaire de cette même these qui se trouve a la Bibliothèque centrale du Muséum national d'Histoire naturelle de Paris est dépourvu de planche, celle-ci ayant manifestement été perdue La planche reproduite ici en fig. 3 est tirée d'un exemplaire de l'édition de 1789 qui se trouve à la Bibliotheque centrale du Muséum national d'Histoire naturelle de Paris On notera l'existence de quelques différences entre les deux planches, dont la plus notable concerne la longueur des branchies de *Siren lacertina*

Source MNHN, Paris

après la publication de cet opuscule, le très clairvoyant D. Ellis a donné une nouvelle histoire avec une excellente figure in Act. angl vol. 56. p. 189. t 9.") (ÖSTERDAM, 1769: 325, 1789: 325)

Le texte dont il est ici question a lui aussi été ignoré par la plupart des auteurs ultérieurs, bien qu'il ait été cité par quelques-uns d'entre eux (p ex : LA CÉPÈDE, 1788 a: 611, 1788 b: 381; SCHNEIDER, 1799 49; DAUDIN, 1803· 272; MERREM, 1820: 188; GRAY, 1825: 216, HOLBROOK, 1842: 102; DUMÉRIL, BIBRON & DUMÉRIL, 1854: 193). Il s'agit d'un texte qui fut lu par John ELLIS le 5 juin 1766 devant la Royal Society de Londres Ce texte permet de reconstituer l'ensemble de l'histoire qui amena un spécimen de cette espèce devant les yeux de LINNÉ et de son élève ÖSTERDAM. Selon ELLIS (1767), c'est durant l'été de 1765 qu'il reçut d'Alexander GARDEN, "of Charles-town South Carolina", trois spécimens (un grand et deux petits) de cet animal extraordinaire et jusqu'alors inconnu des naturalistes Ces animaux sont décrits et deux d'entre eux figurés (fig. 5); à titre de comparaison, des larves de Tritons d'Angleterre sont également représentées. Incertain quant au statut de ces animaux (larves ou adultes?), et à la demande de GARDEN, ELLIS envoya à LINNÉ, à Uppsala, un des deux petits spécimens et la description détaillée du grand spécimen par GARDEN La réponse de LINNÉ, datée du 27 décembre 1765 à Uppsala (Upsal), et probablement traduite du latin par ELLIS (1767: 191-192), est la suivante·

"I received Dr Garden's very rare two-footed animal with gills and lungs. The animal is probably the larva of some kind of lacerta, which I very much desire that he will particularly enquire into

If it does not undergo a change, its belongs to the order of *Nantes*, which have both lungs and gills, and if so, it must be a new and very distinct genus, and should most properly have the name of *Siren*

I cannot possibly describe to you how much this two-footed animal has exercised my thoughts, if it is a larva, he will no doubt find some of them with four feet

It is not an easy matter to reconcile it to the larva of the lizard tribe, its fingers being furnished with claws, all the larvas of lizards, that I know, are without them (*digitis muticis*)

Then also the branchiae or gills are not to be met with in the aquatic salamanders, which are probably the larvas of lizards.

Further, the croaking noise or sound it makes does not agree with the larvas of these animals; nor does the situation of the anus.

So that there is no creature that ever I saw, that I long so much to be convinced of the truth, as what this will certainly turn out to be "

ELLIS (1767) lui-même n'emploie pas le nom générique *Siren* dans le texte de son travail, mais ce nom apparaît sur la planche qui illustre celui-ci (fig. 5). HUNTER (1767), qui est l'auteur d'un deuxième article consacré au même animal paru dans le même volume, ne mentionne pas ce nom Toutefois, en vertu de l'Article 50 du *Code* (ANONYME, 1985), la publication par ELLIS (1767), dans le même travail, d'une description et de dessins de l'animal, et du nom générique *Siren*, ferait de lui, et bien qu'il attribue expressément ce nom à LINNÉ, l'auteur, au sens nomenclatural du terme, de ce nom générique, si son travail avait été publié avant celui d'ÖSTERDAM (1766). Les dates respectives de publication de ces deux travaux doivent donc être établies

Source MNHN, Paris

S. A. N.

SIREN
LACERTINA,

DISSERTATIONE ACADEMICA
ORBI ERUDITO DATA
QUAM VENIA NOB. ET EXPERIENT. FAC. MED.
AD REG. ACAD. UPSAL.
PRÆSIDE
VIRO NOBILISSIMO et EXPERIENTISSIMO
D:NO DOCT. CAROLO
A LINNÉ,
EQUITE AURATO DE STELLA POLARI;
SÆ RÆ MITIS SUEC. ARCHIATRO,
MED. ET BOTAN. PROFESSORE REG. ET ORD. ACAD. PARIS.
PETROPOL. IMPER. N. C. HOLM. UPSAL.
LOND. ANGL. FLOR. BITROL. MONSP. TOLOS. BERNENS. EDINB.
NIDROS. MEMBRO,
PUBLICE VENTILANDAM SISTIT
STIPENDIARIUS REGIUS
ABRAHAMUS ÖSTERDAM,
HOLMIENSIS
IN AUDITORIO CAROLINO MAJORI
DIE XXI JUNIJ ANNI MDCCLXVI.
H. A. M. C.

UPSALIÆ.

Fig. 1. Reproduction de la page de garde de l'édition originale de la dissertation d'ÖSTERDAM (1766) sur *Siren lacertina* (Bibliothèque du Muséum national d'Histoire naturelle, Paris)

Source MNHN, Paris

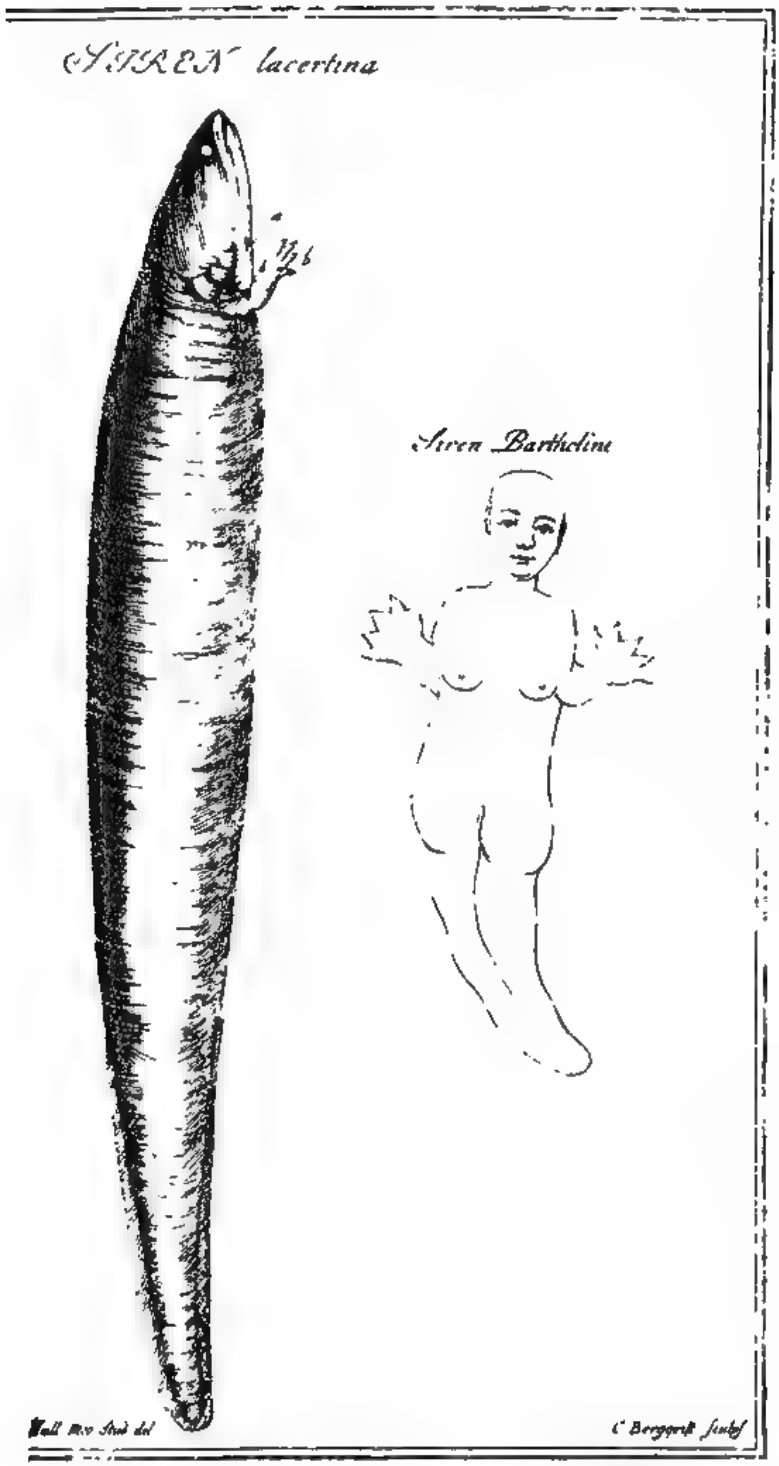

Fig. 2 Reproduction de la planche de l'édition originale de la dissertation d'ÖSTERDAM (1766) sur *Siren lacertina* (Bibliothèque Nationale, Paris).

Source MNHN, Paris

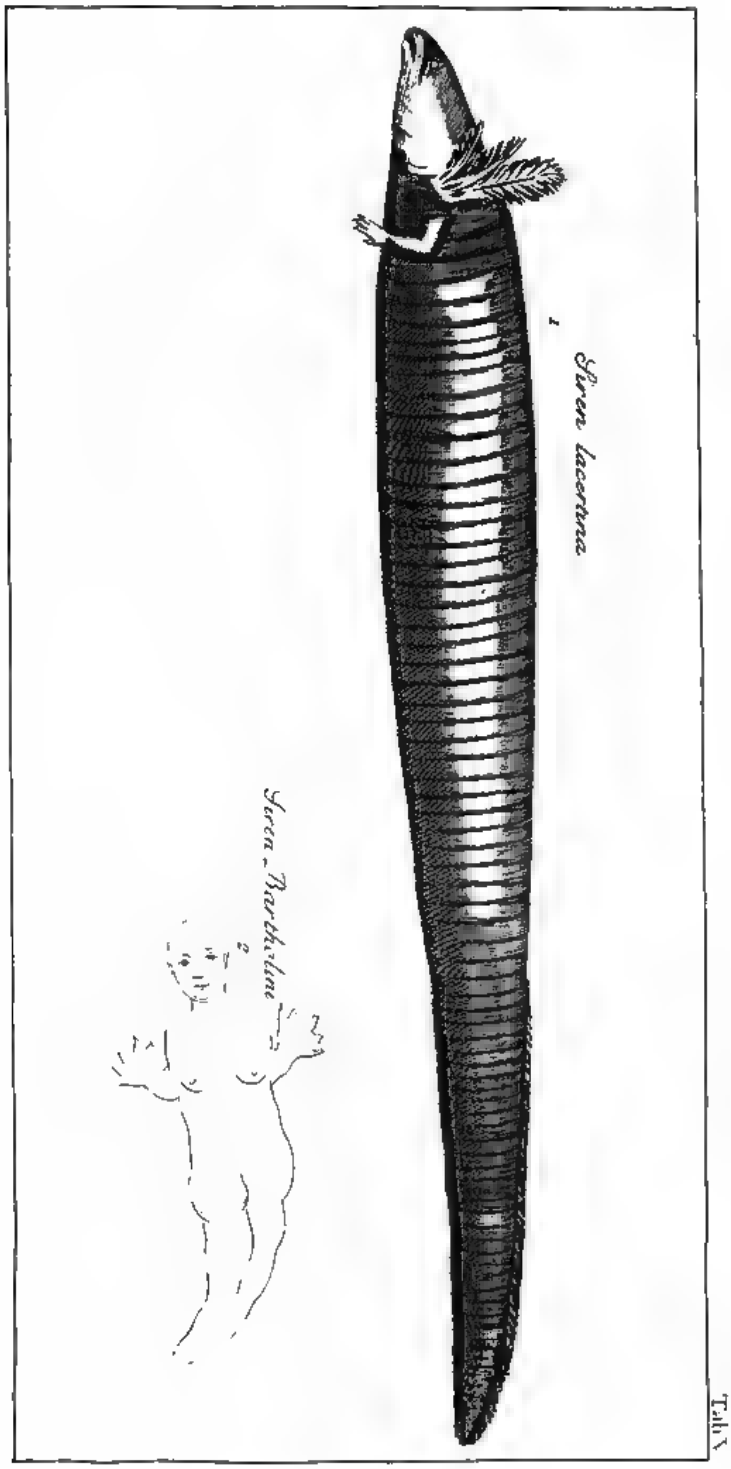

Fig. 3. – Reproduction de la planche V de la troisième version de la dissertation d'OESTERDAM (1789) sur *Siren lacertina* (Bibliothèque du Muséum national d'Histoire naturelle, Paris)

Source MNHN, Paris

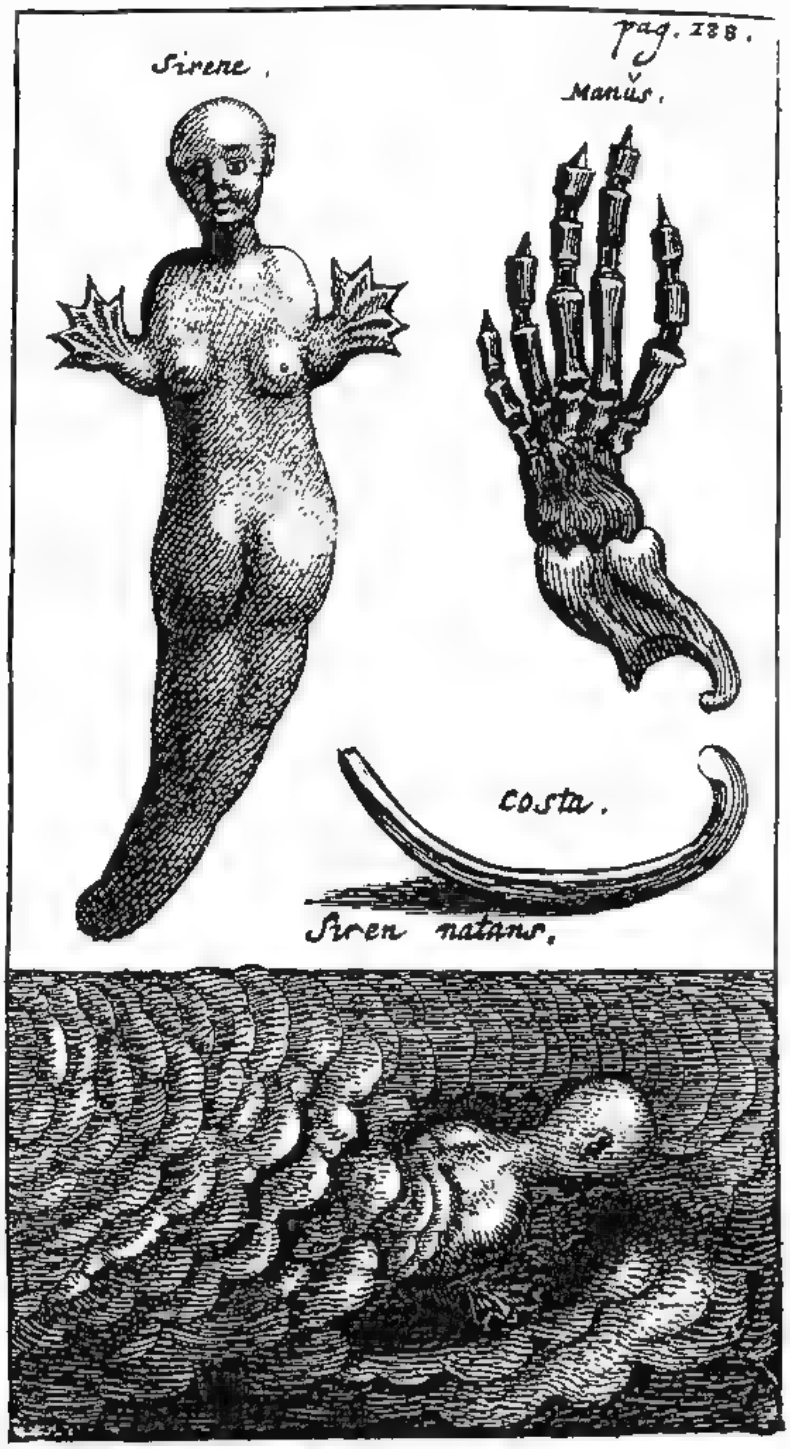

Fig 4 – Reproduction de la planche de la page 189 de BARTHOLIN (1654 c) montrant une "sirène" recueillie dans la "mer du Brésil", cet animal en train de nager et une dissection d'une "main" de celui-ci (Bibliothèque du Muséum national d'Histoire naturelle, Paris).

Source MNHN, Paris

Fig. 5. — Reproduction de la planche IX de l'article d'ELLIS (1767) sur *Siren lacertina* (Bibliothèque du Muséum national d'Histoire naturelle, Paris).

Source MNHN, Paris

Chronologie de ces publications

La communication orale d'Ellis fut faite à Londres le 5 juin 1766, tandis qu'Österdam soutint sa thèse à Uppsala le 21 juin 1766. Toutefois, comme nous l'avons vu, dans la deuxième version publiée de sa thèse, Österdam (1769: 325, 1789: 325) précise que le travail d'Ellis est paru *après* la première publication de sa propre thèse. Ceci semble confirmé par la page de garde du volume **56** ("For the year 1766") des *Philosophical transactions*, qui porte la date de publication de 1767, comme l'ont noté Duméril, Bibron & Duméril (1854: 193) Cette dernière date est du reste très vraisemblable, puisque ce volume, qui fut apparemment publié en une seule fois, comporte des communications qui ont été lues à la Royal Society du 23 janvier au 18 décembre 1766: il est donc peu probable que le volume ait pu paraître en 1766. En l'absence d'indications plus précises sur les dates de publication de ces travaux, il faut suivre l'Article 21 du *Code* (Anonyme, 1985), qui précise que la date à retenir est celle du "dernier jour de l'année" de publication, soit le 31 décembre 1766 pour le travail d'Österdam et le 31 décembre 1767 pour ceux d'Ellis et de Hunter. Par ailleurs, comme nous l'avons vu, il faut considérer le travail de Linné (1766) comme postérieur à celui d'Österdam (1766), qui y est cité en page 371· afin de respecter cette priorité, il faut dater le travail d'Österdam (1766) du 30 décembre 1766 au plus tard et celui de Linné (1766) du 31 décembre 1766 Dans ces conditions, il faut admettre qu'Österdam (1766) est l'auteur, au sens nomenclatural, des noms *Siren* et *Siren lacertina*. Il en résulte que le type porte-nom de cette dernière espèce est le spécimen qu'Ellis avait fait parvenir à Linné et qui est figuré dans le travail d'Österdam (1766, 1769, 1789), qui en est donc l'holotype et type unique, et non pas les spécimens décrits et figurés par Ellis (1767).

Quant au nom du groupe-classe (sensu Dubois, 1984) Meantes, il est apparu pour la première fois dans le livre de Linné (1767), qui en est donc l'auteur au sens nomenclatural. en effet ce nom ne figure pas dans la première version du travail d'Österdam (1766) et n'apparaît que dans la deuxième version de ce travail (Österdam, 1769: 325, 1789: 325), postérieure au livre de Linné (1767). Ce nom n'est pas actuellement considéré comme valide, mais pourrait l'être dans l'avenir, pour désigner un sous-ordre des Urodèles (reconnu par exemple par Duellman & Trueb, 1986 et par Laurent, 1986, sous le nom de Sirenoidea, pour la seule famille des Sirenidae), ou même un ordre à part, comme l'ont suggéré certains auteurs (p. ex. Goin & Goin, 1962).

Problèmes nomenclaturaux

Deux dernières questions méritent discussion d'un simple point de vue nomenclatural.

L'Article 9(11) du *Code* actuel (Anonyme, 1985) précise que "le dépôt d'un document (tel qu'une thèse) dans une collection de documents, une bibliothèque ou d'autres archives" n'a pas "valeur de publication au sens du Code". La thèse d'Österdam (1766) a-t-elle valeur de publication? Ceci ne saurait faire de doute: il s'agit d'un opuscule

Source MNHN, Paris

imprimé, qui fut manifestement envoyé à toutes les grandes institutions scientifiques de l'époque, et qui est expressément cité par LINNÉ (1766: 371; 1767: [xxxvi]) lui-même. Ce texte a ensuite été repris, avec quelques modifications, dans des recueils de thèses soutenues sous la présidence de LINNÉ, recueils qui ont eu eux aussi une large diffusion. A cette époque toutes les thèses une fois soutenues étaient imprimées et diffusées dans le monde comme des publications à part entière. Il ne saurait être question d'appliquer à une thèse publiée à cette époque l'Article 9(11) actuel, qui n'a été ajouté dans la dernière édition du *Code* que pour éviter les problèmes nouveaux créés par la tendance récente de certains auteurs à introduire des noms scientifiques nouveaux dans des thèses ronéotypées et ne faisant l'objet d'aucune diffusion publique.

Le deuxième point problématique est celui de l'espèce-type du genre *Siren*. Bien que, dans le texte original de sa thèse, ÖSTERDAM (1766) ne mentionne que l'espèce *Siren lacertina*, sur la planche qui accompagne ce texte sont figurées deux espèces, *Siren lacertina* et *Siren bartholini*. Ce deuxième nom a-t-il un statut en nomenclature zoologique? La question se pose parce que l'Article 1(b)(1) du *Code* (ANONYME, 1985) précise que "les dispositions du Code ne sont pas applicables aux noms proposés (...) pour des concepts hypothétiques" Comme nous l'avons vu et comme en témoigne son texte ultérieur (1769, 1789), ÖSTERDAM était manifestement incertain de la nature, réelle ou fictive, de cette dernière espèce. Il renvoyait expressément à la description de BARTHOLIN (1654 a-b-c) et reproduisait une des figures de cet auteur. Ce renvoi bibliographique et cette figure constituent manifestement des "indications", au sens de l'Article 12(b) du *Code* (ANONYME, 1985). De plus, cette description et ces figures s'appuyant manifestement sur un spécimen réel, qui avait été capturé et même disséqué, le nom *Siren bartholini* est indubitablement disponible pour l'espèce de Mammifère marin à laquelle appartenait ce spécimen Le nom *Siren bartholini* d'ÖSTERDAM (1766) ne s'applique donc pas à un "concept hypothétique" et n'est pas non plus un nomen nudum. Il faut donc considérer que le genre nominal *Siren* a été créé avec deux espèces nominales incluses, *Siren lacertina* Österdam, 1766 et *Siren bartholini* Österdam, 1766, dont aucune n'était désignée comme espèce-type du genre dans la description originale. L'espèce-type du genre sera donc la première de ces deux espèces nominales à avoir été désignée comme telle par un auteur ultérieur. En l'occurrence, et par chance, il s'agit de *Siren lacertina*, expressément désignée comme type de *Siren* pour la première fois par HARLAN (1826: 321).

CONCLUSION

On trouvera ci-dessous une récapitulation des statuts nomenclaturaux des noms actuellement considérés valides pour désigner les différents taxons auxquels sont attribuées les trois espèces reconnues au sein de la famille des Sirenidae. Ainsi que cela a déjà été noté (DUBOIS, 1987: 126), c'est par erreur que BRAME (*in* FROST, 1985 617) écrit au sujet du nom Sirenidae: "As first formed the group name was Serenina." Il est vrai que le nom subfamilial Serenina apparaît en p. 216 du travail de GRAY (1825), mais en p. 215 du même travail figure le nom Sirenidae avec son orthographe valide actuelle! En ce qui concerne le nom spécifique *Siren intermedia*, qui fut longtemps attribué à LE CONTE (1828), SMITH, SMITH & SAWIN (1975) ont établi qu'il devait être attribué à BARNES (1826).

Source MNHN, Paris

Sous-ordre MEANTES Linné, 1767: [xxxvi], addenda non paginé. – Genre-type par monotypie: *Siren* Österdam, 1766.

Famille SIRENIDAE Gray, 1825: 215. – Genre-type par désignation étymologique implicite: *Siren* Österdam, 1766.

Genre *Pseudobranchus* Gray, 1825: 216. – Espèce-type par monotypie: *Siren striata* Le Conte, 1824.

Pseudobranchus striatus (Le Conte, 1824: 53).

Genre *Siren* Österdam, 1766: 15. – Espèce-type par désignation subséquente de HARLAN (1826: 321): *Siren lacertina* Österdam, 1766.

Siren intermedia Barnes, 1826. 269.
Siren lacertina Österdam, 1766: 15.

REMERCIEMENTS

L'auteur remercie vivement Henri DELORME et Pierre DUBOIS, qui lui ont permis de disposer d'une traduction intégrale des deux textes latins d'ÖSTERDAM. Cette traduction est conservée au Laboratoire des Reptiles et Amphibiens du Muséum national d'Histoire naturelle, où elle est à la disposition de tous les collègues intéressés.

L'auteur remercie également Roger BOUR et un lecteur anonyme pour leurs commentaires enrichissants, et Annemarie OHLER pour la préparation des figures illustrant ce travail.

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International Journal of Batrachology
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Published with the support of
the Muséum national d'Histoire naturelle (Paris, France)
and of the Société Batrachologique de France.

Directeur de la Publication: Alain DUBOIS.

Numéro de Commission Paritaire: 64851.

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Source : MNHN, Paris

25 FEV. 1991

Alytes, 1989-1990, **8** (3-4): 61-120.

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Alytes is indexed in the following data bases: *Biosis, Cambridge Scientific Abstracts, Current Awareness in Biological Sciences* and *The Zoological Record.*

Imprimerie F. Paillart, Abbeville, France.
Dépôt légal: 1er trimestre 1991.

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Source : MNHN, Paris